Compositional and Structural Characteristics of Ontario's Boreal Mixedwoods

by R.V. Popadiouk
H.Y.H. Chen, C. Bowling
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Executive Summary

This report was designed as one of three background documents for the Silvicultural guide to managing spruce, fir, birch and aspen mixedwoods in Ontario's boreal forest (OMNR 2003). This report focuses on the compositional and structural attributes of Ontario's boreal mixedwoods while the other two are literature syntheses of the Dynamics of North American boreal mixedwoods (Chen and Popadiouk 2002) and silvicultural practices in boreal mixedwoods (Palmer 2003). Specifically, this report addresses:

- how long stands take to reach different stages of stand development in Ontario's boreal mixedwoods, and
- describes stand composition and density, sapling and seedling density, understory vegetation, organic horizons and snags in relation to stand development and soil condition.

We gathered four databases of long-term permanent sample plots established by American Can Pulp and Paper Company, Kimberly Clark of Canada, Spruce Falls Power and Paper Company, and the Ontario Ministry of Natural Resources Growth and Yield program. We also gathered two databases of temporary sample plots from the Forest Ecosystem Classification programs for northeastern and northwestern Ontario. Based on Ontario's definition of boreal mixedwood sites, plots with soil moisture regimes from 2 to 5, from ecosites 3, 6c, 7c, 5m, 6m, 7m, 5f, 6f, 7f, 9r and 10 in northeastern Ontario and ecosites 14, 16, 19, 20, 21, 22, 23, 25, 26, 27, 28, 29, 30, 31, 32 and 33 in northwestern Ontario, were selected for analysis. This selection resulted in a total of 640 plots, each with one to six measurements, totalling 1033 measurements. These plots covered a wide geographic range of Ontario's boreal forest on four broad soil groups (i.e. sandy to coarse loamy, medium loamy to silty, fine loamy to clayey, and moist mineral) and three of the four stand development stages (i.e. stem exclusion, canopy transition and gap dynamics). There were no plots at the stand initiation stage and the number of plots at the gap dynamics stage were small.

Key findings of this report include:

- Stand age defined as time since stand establishment date increases from exclusion to transition to gap dynamics stage. The mean age was 78.8 years for the stem exclusion stage, 86.0 years for the transition stage and 156.4 years for the gap dynamics stage.
- Stand basal area increased with stand development from exclusion to transition to gap dynamics. Stand basal area was generally greater on medium and fine soils than on coarse and moist mineral soils.
- Stand composition changed with stand development as black spruce, trembling aspen, jack pine, white birch and balsam poplar dominated the stands at the stem exclusion and transition stages while black spruce, white spruce, balsam fir, white birch and white cedar dominated the stands at the gap dynamics stage. For the sub-canopy stratum, black spruce, balsam fir, trembling aspen, white birch, jack pine and white spruce dominated at the stem exclusion and transition stages while balsam fir, white cedar, white birch, black spruce and white spruce dominated at the gap dynamics stage.
- Stand density decreased from stem exclusion to transition to gap dynamics stage on coarse, medium and moist mineral soils. Stand density on fine soils was lowest at the stem exclusion stage and did not differ among stand development stages.

- The most frequently occurring saplings were balsam fir and black spruce, followed by white spruce and white birch while white cedar saplings were frequent only at the gap dynamics stage and trembling aspen and balsam poplar saplings were frequent at the stem exclusion and transition stages. Seedling frequency showed a similar trend except that white cedar seedlings were infrequent. Total seedling density was higher than total sapling density for all stand development stages and broad soil groups, except for the exclusion stage on fine soils where the opposite was found.
- Shrubs and non-woody vegetation occurred frequently on all sites and at all stand development stages with a mean percent shrub cover of 30 percent and a mean percent non-woody vegetation cover of 70 percent. Shrub cover was significantly higher at the gap dynamics stage than the exclusion and transition stages. Among non-woody vegetation, herbs and mosses were the most abundant. Mean depth was lower at the transition stage than at the other two stages on coarse and moist soils. Mean depth did not differ amongst stages for medium and fine soils.
- Mean depth of the organic layer ranged from 7 to 15 cm. Depth of humus layer was significantly greater at the gap dynamics stage than at the exclusion and transition stages. Mor was the most frequently occurring humus form, followed by moder. Mull occurred only at the exclusion and transition stages with a frequency <5 percent.
- Snag density varied greatly among stand development stages and broad soil groups with small snags (dbh 10–20 cm) accounting for the majority. Snags of early-successional jack pine, trembling aspen and balsam poplar occurred mostly at the exclusion and transition stages, mid-successional white birch and black spruce occurred at all stages and late-successional white spruce, balsam fir and white cedar were most frequent at the gap dynamics stage.

Recommendations

We make the following specific recommendations for future data collection with respect to improving our understanding of the compositional and structural characteristics of Ontario's boreal mixedwood forest.

Recommendation 1

Future efforts need to be undertaken through provincial programs such as Growth and Yield, to fill gaps and improve our understanding of stand initiation and gap dynamics stages in Ontario's boreal mixedwood forest. Existing databases have few or no plots established in these stages

Recommendation 2

The increasing use of historical databases to address new knowledge gaps outlines the inherent problems in using these databases to answer questions which they were not originally designed to answer. This requires a standardized method of describing forest ecosystems that is being addressed in the current growth and yield and ecosystem classification methodologies. A method similar to that used in British Columbia (B.C. Ministry of Environment, Lands, and Parks and Forests 1998). Revisiting plots to collect data that is not currently available is another option.

Recommendation 3

The small number of sample plots available for stand attributes such as sapling and seedling characteristics, shrubs and non-woody vegetation and snags, did not allow us to address potential ecological differences among eco-regions and stands initiated with different compositional types. We recommend that as more data becomes available through the Growth and Yield Program, that we update this report, recognizing that climate and initial compositional type may significantly affect stand dynamics.

Recommendation 4

We used the chronosequence approach to study stand dynamics. Future efforts can use repeated measurements from the growing number of long-term permanent plots from the Growth and Yield Program.

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INTRODUCTION

Canada's boreal forests are regulated by various large-scale stand-replacing wildfires (Bergeron 1991, 2000, Johnson 1992) and smaller-scale patch disturbances (Frelich and Reich 1995, Kneeshaw and Bergeron 1998, McCarthy 2001, Chen and Popadiouk 2002). Forest resource management in Ontario and elsewhere in Canada has adopted the concept of natural disturbance based management (NDBM) (Davis *et al.* 2001, OMNR 2001, Harvey *et al.* 2002) as it is the closest possible surrogate to natural processes (Burton *et al.* 1992, CFSA 1994). Under the NDBM paradigm, sustainability of managed forest landscapes is evaluated based on whether forest management activities maintain forest composition and age structure within the bounds of natural variation (OMNR 1996, Davis *et al.* 2001). At the stand level, development under natural disturbances and associated processes is considered as a model for guiding silvicultural interventions for managing Ontario's boreal mixedwood forests (OMNR 2003).

In Canadian boreal forests, various studies have significantly advanced our understanding of stand dynamics of boreal mixedwood forests (e.g. Bergeron 1991, 2000). Based on a comprehensive literature review, Chen and Popadiouk (2002) identified the following four stand development stages (SDSs) of boreal mixedwoods based on distinct stand structure, composition and ecological processes: stand initiation, stem exclusion, canopy transition and gap dynamics.

Stand Initiation – After a stand-replacing disturbance (e.g. fire), pioneer tree species such as trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) B.S.P.), will usually (St. Pierre *et al.* 1992, Johnson *et al.* 2004) colonize the available growing space, within five years of a disturbance.

Stem Exclusion – After all the available growing space in the canopy is fully occupied by trees, inter- and intra-species competition occurs as individual trees grow. Intense competition and lack of available growing space prevents further establishment of new stems. Vertical canopy stratification often takes place at a later phase of this stage. The latter part of this stage includes the understory re-initiation stage of Oliver and Larson (1996).

Canopy Transition – The intense competition between stems comes to an end. The start of this stage is defined by tree mortality because of longevity or damage from non-stand-replacing disturbances and the creation of canopy gaps. These gaps allow shade-tolerant conifers from the understory and intermediate canopy to take over the main canopy. New individuals can also establish in these gaps. Structural characteristics of this stage include canopy gaps as well as a stratified canopy. This stage ends when all of the individuals from the initial cohort have died.

Gap Dynamics – Trees are established in the absence of stand-replacing disturbances within the stand. Growing space is available in all strata because of the death of individual trees or groups of trees. This stage is structurally characterized by a mosaic canopy, dominated by shade-tolerant species, usually spruce (*Picea* spp.), balsam fir (*Abies balsamea* (L.) Mill.) and eastern white cedar (*Thuja occidentalis* L.). Gaps are occupied by shade-intolerant and (or) shade-tolerant trees and (or) shrubs such as mountain maple (*Acer spicatum* Lam.), beaked hazel (*Corylus cornuta* Marsh.), speckled alder (*Alnus incana* ssp. *rugosa* (Du Roi) Clausen), raspberries (*Rubus* spp.) and willows (*Salix* spp.), depending on local site conditions.

In this paper these stages will be referred to as initiation, exclusion, transition and gap stages. Such a classification provides a qualitative description of boreal mixedwood stand development. However, quantitative knowledge of species composition and structure of

boreal mixedwoods in relation to stand development stage is essential for forest managers to make silvicultural decisions (OMNR 2003). The purpose of this report was to gain a better understanding of the compositional and structural attributes of Ontario's boreal mixedwoods, and to serve as a companion to the Silviculture guide to managing spruce, fir, birch and aspen mixedwoods in Ontario's boreal forest (OMNR 2003). Specifically, our objectives were to:

- Determine how long stands take to reach different stages of stand development in Ontario's boreal mixedwoods.
- Characterize stand composition, stand density, sapling and seedling density, understory vegetation, organic horizons and snags in relation to stand development stage and soil condition.

Material and Methods

Study Area and Databases

Six databases from Ontario's boreal forest were used in this study, including long-term permanent sample plots established by American Can Pulp and Paper Company—now James River-Marathon Corporation, Marathon (American Can); Kimberly Clark of Canada, Longlac (Kimberly Clark); Spruce Falls Power and Paper Company, Kapuskasing (Spruce Falls); and the Ontario Ministry of Natural Resources Growth and Yield (G&Y) program and temporary sample plots from the Northeast Forest Ecosystem Classification (NE-FEC) and the Northwest Forest Ecosystem Classification (NW-FEC) programs for Ontario (Table 1). These plot networks covered a wide geographic area (Figure 1), representing diverse forest cover types, landforms, topographic positions, soil textures and soil moisture regimes that are found in Ontario's boreal forests.

Table 1. Characteristics of Ontario's boreal mixedwood stands used in analysis.*

Characteristic	American Can	Kimberly Clark	Spruce Falls	OMNR G&Y	NE-FEC	NW-FEC
Number of plots (total measurements)	27 (149)	59 (302)	5 (38)	67	228	249
Hills (1960) ecoregions	3E, 3W	3W	3E	3E, 3W, 4E, 4S, 4W	3E, 4E	3E, 3S, 3W, 4S, 4W
Soil textures	Medium sand to clay	Sand to clay	Sand to clay	Sand to clay	Sand to clay	Sand to clay
Soil moisture	Fresh to moist	Fresh to moist	Fresh to moist	Fresh to moist	Fresh to moist	Fresh to moist
Size of plots (ha)	0.04 to 0.08	0.08	0.24 to 0.4	0.12	0.01	0.01 or wedge prism sweep
Measurement period (yr)	1952–2000	1952–1990	1930–1986	1992–1997	1980–1995	1983–1987

* Note: Geographical pattern of the sample plot locations are presented on Figure 1.

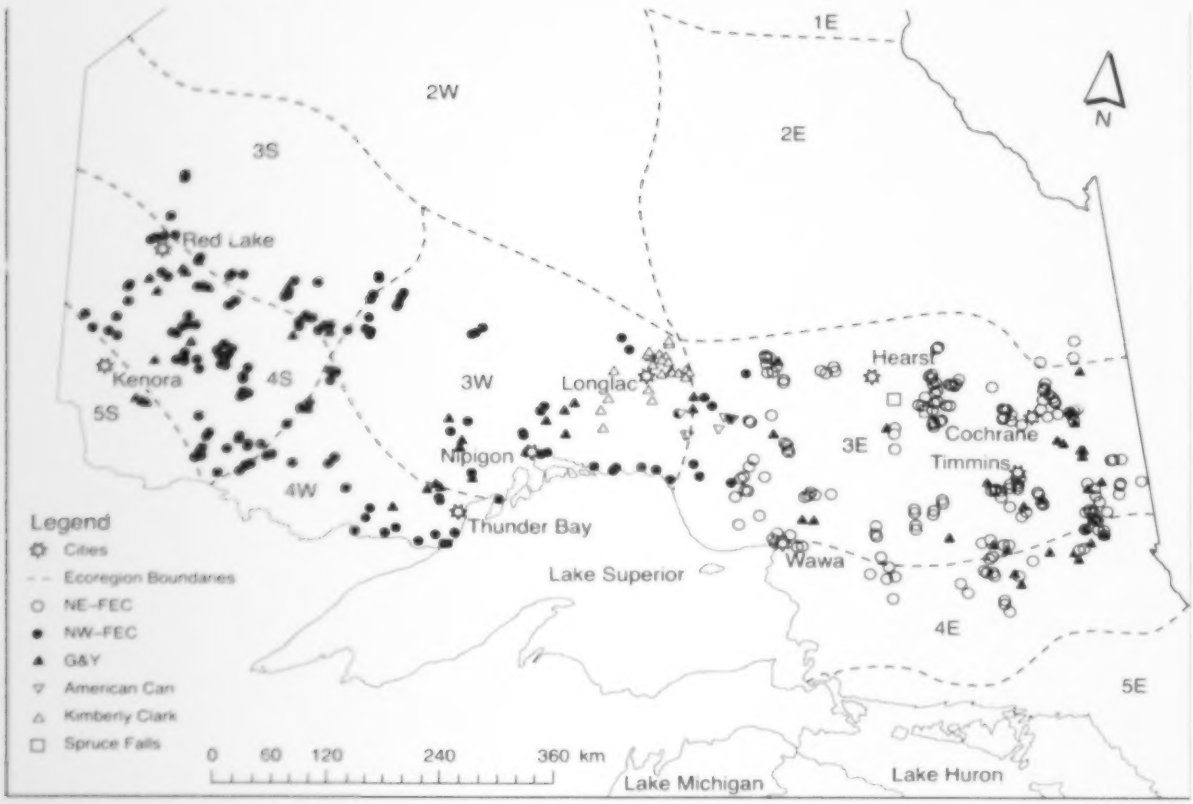

Figure 1. Sample plot location.

Based on the definition of boreal mixedwood sites (MacDonald 1995, OMNR 2003), we selected sites with soil moisture regimes from 2 to 5, from ecosites 3, 6c, 7c, 5m, 6m, 7m, 5f, 6f, 7f, 9r and 10 in northeastern Ontario (Taylor *et al.* 2000) and ecosites 14, 16, 19, 20, 21, 22, 23, 25, 26, 27, 28, 29, 30, 31, 32 and 33 in northwestern Ontario (Racey *et al.* 1996). Further selection involved removal of plots that had silvicultural treatments of any type, and plots from earlier measurements that identified trees only at the genus level. This selection resulted in a total of 640 plots with the number of measurements for each plot varying from one to six, for a total of 1033 measurements. In the long-term permanent sample plots, the number of repeated measurements ranges from two to six, usually at five-year intervals. We assumed that all measurements were independent although some plots were repeatedly measured with an autocorrelation.

Determination of Stand Attributes

Stand establishment date (time since the last stand-replacing disturbance) was recorded for most permanent plots. Temporary plots only documented breast-height ages of some selected trees. In the absence of stand establishment dates, the age of the oldest pioneer tree (or any other tree if pioneer species were missing) was used to determine stand establishment date using the models developed by Vasiliauskas and Chen (2002). It was not possible to determine the stand establishment date for 14 plots, so stand age was analyzed for 1019 out of 1033 measurements (see Appendix 1 for sample sizes of all stand attributes).

Diameter at breast height (dbh), taken at 1.3 m, was measured on every tree in all plots. Measurements were taken to the nearest millimetre or were recorded by one-inch diameter classes, depending on the database. Minimum diameters were 2.5 cm or one inch for all databases. Tree height was only measured in some plots and the data were not used in this report.

Crown class was only identified for trees in the G&Y database and the last measurement of the American Can database. For all other databases, K-means cluster analysis (Euclidean distance, SYSTAT 10) was used to classify trees into canopy and sub-canopy classes in each sample plot based on measured dbh (Appendix 2). The accuracy of this method was evaluated using discriminant analysis of the G&Y plots, in which both crown class (Hayden *et al.* 1995) and dbh were known. We found that the K-means cluster analysis correctly classified 77 percent of the canopy stems (i.e. emergent, dominant and co-dominant crown classes) and 91 percent of the subcanopy stems (i.e. intermediate, suppressed and understory crown classes) (Appendix 2). Canopy and subcanopy characteristics were determined using field crown class measurements for the G&Y and American Can plots and the results of K-means cluster analysis for plots from other databases.

Saplings and seedlings: saplings are tree stems >1.3 m in height and <2.5 cm in dbh. Seedlings are tree stems ≥0.5 m but smaller than saplings. Seedlings <0.5 m tall were not recorded in any databases. Numbers and percent covers of saplings and seedlings were recorded in the American Can and G&Y databases. The NE–FEC data included saplings percent cover. The NW–FEC data included the percent cover of seedlings and saplings with heights between 0.5 and 2.0 m, and this was incorporated into the sapling percent cover analyses. No sapling and seedling measurements were recorded in the Kimberly Clark and Spruce Falls databases.

Shrub percent cover was recorded in all databases except Kimberly Clark and Spruce Falls. A total of 70 shrub species were found in boreal mixedwood plots. Shrub cover was split into three height classes: tall (>2 to 10 m tall), medium (0.5 to 2.0 m tall) and low (<0.5 m tall) in American Can, G&Y and NW–FEC data. The same species in the same plot can contribute percent cover to one, two or three height classes. Total shrub cover was determined as the cumulative percent cover of all shrub species and all size classes in each plot. The NE–FEC database did not differentiate the size of shrubs. Consequently, the analysis of shrub cover by height classes did not include the NE–FEC database.

Non-woody vegetation percent cover: American Can and G&Y databases recorded percent cover of non-woody plants by vegetation group (herbs, grasses and sedges, Sphagnum and lichens). The NE–FEC and NW–FEC recorded percent cover by species and each species was classified to one of these classes. Non-woody vegetation were not recorded in the Kimberly Clark and Spruce Falls databases.

Depths of organic horizons (L, F and H) and humus forms were recorded in American Can, G&Y, NE–FEC and NW–FEC, but not in the Kimberly Clark and Spruce Falls databases. Humus forms were classified as mor, moder and mull.

Snags by species, decay class and dbh were recorded in the American Can, G&Y and NE–FEC plots. Other databases did not include snag records.

Soil moisture regime and soil texture were recorded in all databases. Soil texture classes and sub-classes were aggregated into several distinct groups according to the Ontario Centre for Soil Resource Evaluation (1993). In the G&Y plots, more than one soil sample was used to describe a plot, resulting in soil moisture regime variations that in some cases exceeded three

or more classes within a plot. The most frequently occurring moisture regime was used to represent plot-level soil moisture regime.

Classification of Stand Development Stage

The stand development stage (SDS) for each plot was determined by using the following algorithm. If one or more pioneer species (i.e. jack pine, trembling aspen, balsam poplar (*Populus balsamifera* L.), white birch (*Betula papyrifera* Marsh.) or black spruce (*Picea mariana* (Mill.) B.S.P.) were not present in the canopy layer, the plot was classified as the gap dynamics stage. If pioneer species were present in the canopy layer (dominants and co-dominants) but their ages were significantly younger (at least two age classes, 40 years) than that of any late successional species, these shade intolerant species were considered as having established under a gap environment, and the plot was classified into the gap dynamics stage. If the plot was not in the gap dynamics stage, we analyzed vertical stand structure by species and crown class to determine if the plot was in the stem exclusion or canopy transition stage. If the canopy layer consisted of only pioneer species, the plot was classified as the stem exclusion stage. If both pioneer and late successional species (i.e. white spruce (*Picea glauca* (Moench) Voss), balsam fir, eastern white cedar and conditionally white birch and black spruce when they were the more shade-tolerant species in a plot and clearly younger than jack pine, trembling aspen or balsam poplar in the plot by one age class) were present in the canopy, the plot was classified as the canopy transition stage. No selected boreal mixedwood plots were at the stand initiation stage.

Classification by Broad Soil Group

Soil textures and moisture regimes were used to classify plots into four broad soil groups (BSGs) (Table 2) (Racey *et al.* 1996, Taylor *et al.* 2000). They were 1) sandy to coarse loamy, 2) medium loamy to silty, 3) fine loamy to clayey and 4) moist mineral. These four groups will be referred to as coarse, medium, fine and moist mineral soils in this report.

Table 2. Characteristics of the four broad soil groups used in the study.

Broad soil group	Soil moisture regime	Depth to mottles (cm)	Soil texture	Ecosite types
Coarse	2–3	>60	Sandy to coarse loamy soils	NE: 3, 6c, 7c NW: 14, 16, 19, 20, 21
Medium	2–3	>60	Medium loamy to silty soils	NE: 5m, 6m, 7m NW: 25, 27, 28
Fine	2–3	>60	Fine loamy to clayey soils	NE: 5f, 6f, 7f NW: 26, 29, 30
Moist mineral	4–5	<60	All soil textures	NE: 10, 9r NW: 22, 23, 31, 32, 33

Data Analysis

Stand basal areas (m^2/ha) for all fixed area plots were calculated as the sum of basal areas of each tree in the plot and scaled up to a hectare basis. Stand is defined as canopy plus sub-canopy in the analysis. For prism plots, stand basal area was calculated as the number of stems multiplied by the basal area factor (BAF 2). The BAF is the number of square metres of basal area per hectare each counted stem represents. For prism plots, stand density was calculated according to Avery and Burkhart (2002).

Stand species compositions are evaluated by relative species frequency (RSF), percent basal area (PBA) and importance value (IV). RSF is calculated as presence or absence of a species for each stand. PBA is calculated as percent basal area of a species in a stand. Only stands with >0 percent basal area of a specific species were included to estimate the difference in the percent basal area of the species among SDSs and BSGs. Such a selection allowed evaluation of an individual species dominance when present. Species importance value measures both relative frequency and percent basal area (Smith 1980). Importance value for each species was calculated for all plots including those without presence of the species as:

$$IV = \frac{RSF + PBA}{2} \qquad [1]$$

To determine if species composition and stand structure differ with SDS and BSG, we used the following analysis of variance model:

$$Y_{ijk} = \mu + D_i + S_j + D \times S_{ij} + \varepsilon_{k(ij)} \qquad [2]$$

where Y_{ijk} is stand age, stand basal area, species composition by basal area, stand density, density of saplings and seedlings, shrub cover, non-woody vegetation cover, depth of organic horizons, or snag density; μ is the overall mean of an evaluated parameter; D_i (i = 1, 2 and 3) is the stand development stage; S_j (j = 1, 2, 3 and 4) is the broad soil group; $D \times S_{ij}$ is the interaction between stand development stage and broad soil group; ε is the error term. The General Linear Model (GLM) procedure was used to determine effects and to test hypotheses (SYSTAT 10).

Categorical dependent variables were analyzed by the following loglinear model:

$$SP_n \times D_i \times S_j = D_i + S_j + D \times S_{ij} \quad [3]$$

where SP_n is the frequency of tree species, sapling, seedling, shrub, non-woody vegetation type and humus forms; D_i, S_j and $D \times S_{ij}$ are the same in model [2]. In addition, one-way frequency tables were used to determine frequencies of the analyzed categories within each combination of SDS and BSG (SYSTAT 10).

Results and Discussion

Stand Age

On all soils except fine soils, stand age increased with SDS from exclusion to transition to gap stage (Figure 2). Mean age (and range) for the exclusion stage was 79 (11–196) years, for the transition stage was 86 (22–214) years, and for the gap stage was 156 (97–224) years.

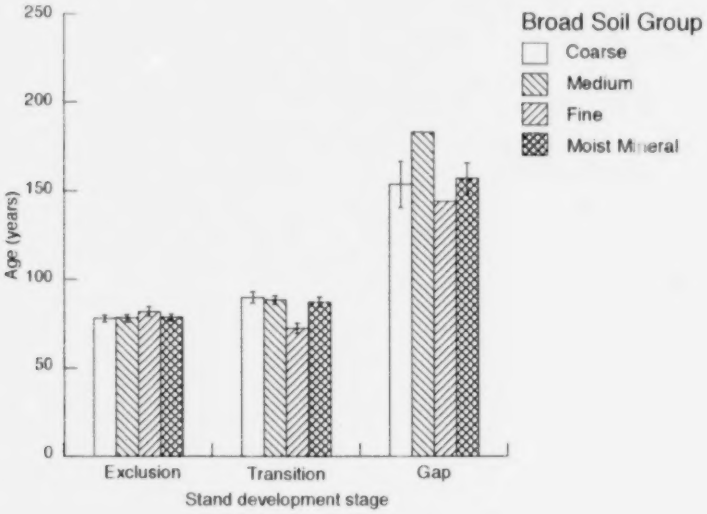

Figure 2. Stand age in relation to stand development stage and broad soil group.

From an individual stand perspective, stand age continuously increases with SDS (Oliver and Larson 1996, Chen and Popadiouk 2002) and our findings agree with this perspective except for fine soils. While our analysis focused on understanding all cover types on boreal mixedwood sites, the similarity in stand ages between exclusion and transition stages on fine soils may reflect a confounding relationship between SDS and cover type. For example, stands initiated with trembling aspen may reach the transition stage earlier than stands initiated with black spruce (Vasiliauskas and Chen 2002). Further, the pattern of stand age on fine soils may reflect that some of the stands classified as exclusion stage might have had a delay in recruitment of shade tolerant species into their understory, resulting in a longer stem exclusion stage. Such findings indicated that using the chronosequence approach to characterize stand dynamics needs careful interpretation of the results. As expected, the mean age of the gap stage was similar to the reported longevity of pioneer species (Harvey *et al.* 2002). The youngest age for the gap stage was 99 years, which was older than ages of 40 to 80 years reported for some mixedwoods in Alberta (Cumming 2001).

Stand Basal Area

Stand (canopy and sub-canopy) basal area varied significantly among SDSs and BSGs with a significant interaction between SDS and BSG (Table 3). On medium and fine soils, stand basal area increased with SDS although stand basal areas did not differ significantly between exclusion and transition stages on medium soils. On coarse and moist mineral soils, stand basal area did not change with SDS (Figure 3). Regardless of SDS, stand basal area was generally higher on medium and fine soils.

Table 3. P-values from analysis of variance of stand, canopy and sub-canopy basal areas (m^2/ha) by stand development stage (D_i) and broad soil group (S_j).

Source	Stand	Canopy	Sub-canopy
D_i	<0.001	<0.001	0.006
S_j	<0.001	0.010	0.006
$D \times S_{ij}$	<0.001	0.001	0.080

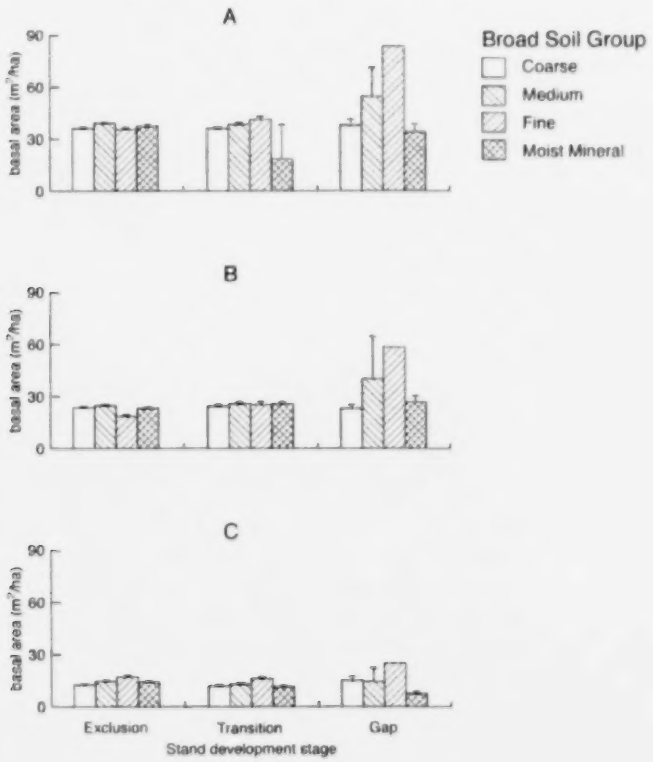

Figure 3. Basal area in relation to stand development stage and broad soil group for: A) stand, B) canopy and C) sub-canopy.

Similar to stand basal area, canopy basal area significantly varied with SDS and BSG with a significant interaction between the two factors (Table 3 and Figure 3). Canopy basal area increased from stem exclusion to canopy transition stage (Figure 3). Further increase from canopy transition to gap dynamics stage characterized fine and medium soils. On coarse soils, canopy basal area did not vary significantly among SDSs.

Sub-canopy basal area varied significantly with SDS and BSG with a marginally significant interaction of the two factors (Table 3 and Figure 3). It increased from coarse, medium to fine soils. In relation to SDS, sub-canopy basal area increased on coarse, medium and fine soils and decreased on moist soils.

Changes in basal area followed a similar pattern at the stand and canopy levels, indicating that dominant and codominant trees accounted for the largest proportion of stand basal area. Few papers have given basal areas for stands at the gap stage. Hely *et al.* (2000) found a stand basal area of 15 m^2/ha in a 236-year-old white cedar stand. A recent study on natural succession in northeastern Ontario's boreal forest indicated that stand basal area at the gap stage varied from 8.8 to 42.6 m^2/ha and can also increase or decrease depending on tree species dominance (Chen and Vasiliauskas, unpublished data). The lack of decrease in basal area from transition to gap stage could be an artefact of sampling, as old open stands with large gaps were often not surveyed.

Sub-canopy basal areas were highest on medium and fine soils, consistent with Yarie (1983) and MacDonald (1995). Sub-canopy trees, which do not receive full sunlight, predictably had less basal area than canopy trees. Changes in sub-canopy basal areas with SDS were different from those in the canopy. A decrease at the transition stage coincided with an increase in the canopy conifer component, most likely due to sub-canopy stems growing into the canopy.

Stand Composition

Results

Species Frequency

Eight species (jack pine, trembling aspen, balsam poplar, white birch, black spruce, white spruce, balsam fir and white cedar) occurred frequently on boreal mixedwood sites (Figure 4). Infrequently occurring species included red pine (*Pinus resinosa* Ait.), white pine (*P. strobus* L.), tamarack (*Larix laricina* (Du Roi) K. Koch), red maple (*Acer rubrum* Lam.), black ash (*Fraxinus nigra* Marsh.) and largetooth aspen (*Populus grandidentata* Michx.), and these were grouped into the other species category in analysis. The frequency of each species, at either the stand or sub-canopy levels, differed significantly among SDSs and BSGs, and the interactions of SDS and BSG on species frequency were significant for all species ($P < 0.01$).

At the stand level, of the three least shade-tolerant species, jack pine and trembling aspen had higher frequencies than balsam poplar. Jack pine had a high frequency on coarse, medium and moist mineral soils and had lowest frequency on fine soils. Its frequency decreased from exclusion to transition stage on all soils but increased on medium soils (Figure 4). Trembling aspen frequency increased from exclusion to transition stage on coarse and fine soils, decreased on medium soils and did not change on moist soils (Figure 4). Less than five percent of the stands on coarse soils and less than 1/3 of the stands on other soils had balsam poplar.

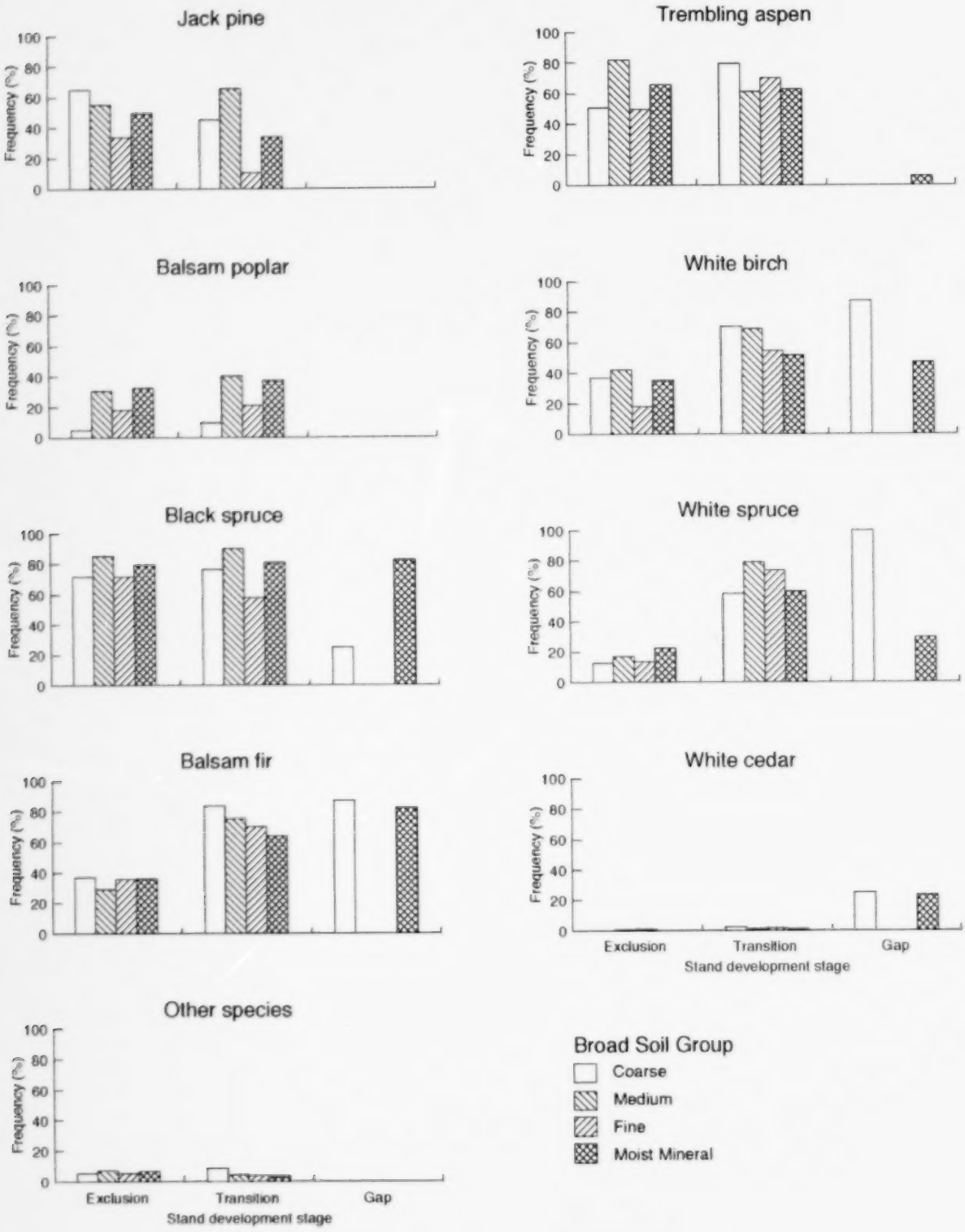

Figure 4. Species-specific frequency at stand level in relation to stand development stage and broad soil group.

Intermediate shade-tolerant white birch and black spruce were found on all BSGs and SDSs (Figure 4). The lowest frequency of white birch was on fine soils at the exclusion stage (Figure 4). White birch frequency increased from exclusion to transition stage with a greater increase on fine and moist soils than on coarse and medium soils. There was a further increase in frequency on coarse and moist soils at the gap stage while birch was absent from plots on medium and fine soils at gap stage. Black spruce had the highest frequency of all species at the exclusion stage on all soils (Figure 4). At the transition stage, frequency of black spruce increased slightly on coarse, medium and moist soils, but decreased on fine soils. At the gap stage, black spruce frequency ranged from 25 percent on coarse soils to over 80 percent on moist soils. Frequencies of late successional white spruce, balsam fir and white cedar increased from exclusion to transition to gap stage except for white spruce at the gap stage (Figure 4). At the gap stage on moist soils, white spruce frequency was only about one-third that of black spruce. The frequency of other species was generally <5 percent (Figure 4).

The frequency of pioneer species in the sub-canopy was slightly lower than at the stand level (Figures 4 *vs.* 5), but their relationships to SDS and BSG were similar to those at the stand level. The frequencies of mid- and late-successional species in the sub-canopy followed similar patterns to their frequency at the stand level (Figures 4 and 5).

Percent Basal Area

The effects of SDS and BSG on percent basal areas varied with tree species and at the stand and sub-canopy levels (Table 4). At the stand level, jack pine percent basal area significantly decreased from exclusion to transition stage on coarse, medium and fine soils but did not change on moist soils. Trembling aspen percent basal area was significantly higher on fine soils than on other soil types, but did not differ between exclusion and transition stages (Table 4 and Figure 6). Similar to trembling aspen, balsam poplar percent basal area was significantly affected by BSG, but not by SDS (Table 4 and Figure 6). On fine and moist soils, balsam poplar percent basal area was significantly higher than on coarse and medium soils.

At the stand level, percent basal area of both white birch and black spruce differed significantly among BSGs and SDSs and with a significant interaction between the two factors (Table 4). White birch percent basal area decreased significantly on coarse soils, increased significantly on fine and moist soils, and did not change on medium soils with stand development (Figure 6). Black spruce percent basal area significantly decreased with stand development on all soils except moist soils. It declined from 40 to 60 percent at the exclusion stage, to 20 to 30 percent at the transition stage. Fine and moist soils had a higher black spruce percent basal area.

Percent basal area of late successional white spruce, balsam fir and white cedar significantly increased with stand development (Table 4 and Figure 6). On coarse, medium and moist soils, white spruce percent basal area significantly increased from exclusion to transition to gap stage (Figure 6). On fine soils it increased only from exclusion to transition stages. Fine soils had the highest white spruce percent basal area at the exclusion and transition stages, but coarse soils had the highest percent basal area at the gap stage. Balsam fir percent basal area varied significantly with SDS, but did not change among BSGs (Table 4 and Figure 6). All soil types showed a significant increase in percent basal area from exclusion to transition stages with a further increase for coarse and medium soils from transition to gap stage. White cedar percent basal area marginally increased with stand development, but did not change with BSG. A lack of replicates at the gap stage precluded further examination (Table 4 and Figure 6).

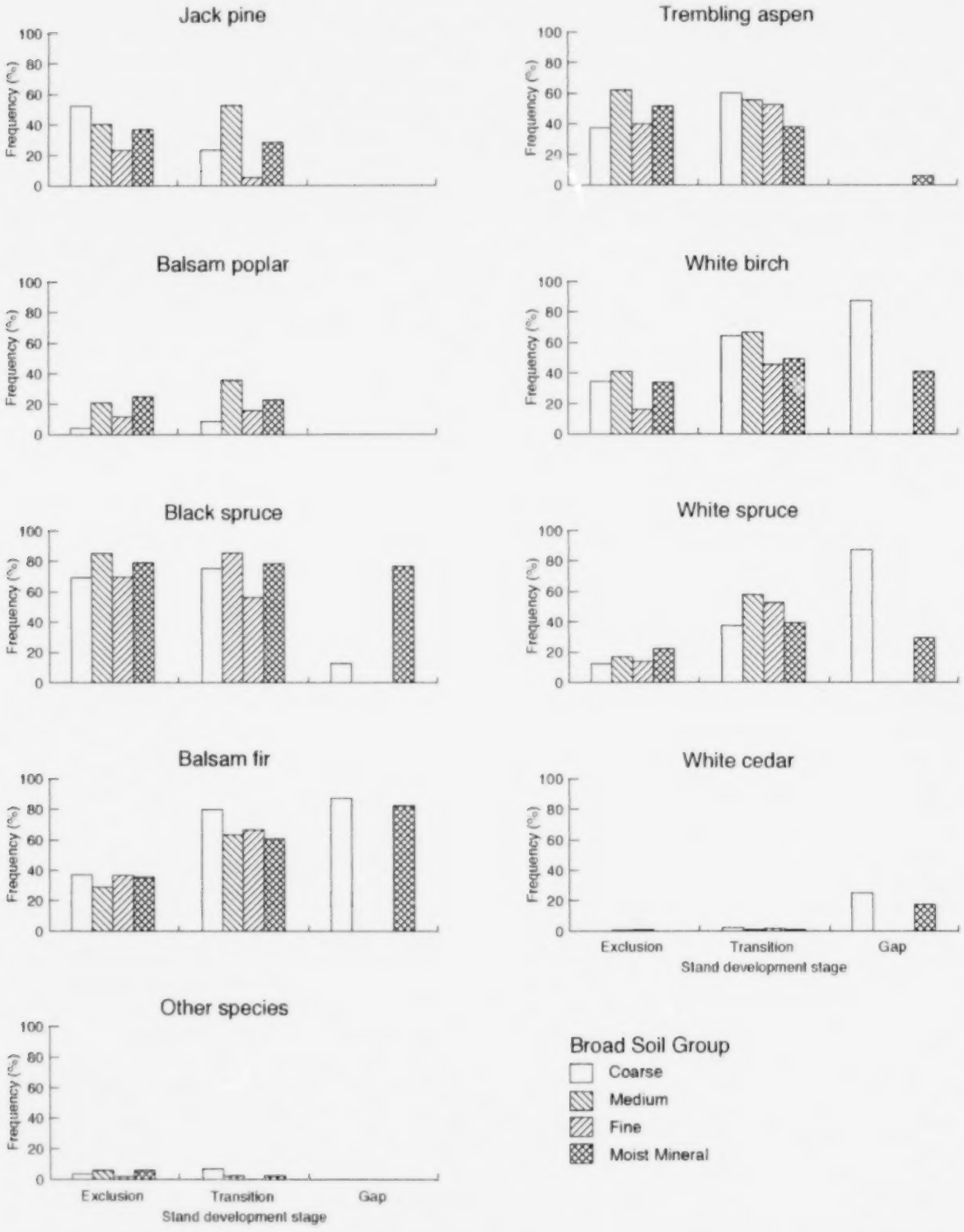

Figure 5. Sub-canopy species-specific frequency in relation to stand development stage and broad soil group.

Table 4. P-values from analysis of variance for species-specific stand and sub-canopy basal areas (m^2/ha) by stand development stage (D_i) and broad soil group (S_j).

Source	Jack pine	Trembling aspen	Balsam poplar	White birch	Black spruce	White spruce	Balsam fir	White cedar	Other species
Stand									
D_i	0.002	0.61	0.32	0.50	<0.001	<0.001	<0.001	0.1	0.72
S_j	0.68	0.004	0.006	0.08	0.005	0.02	0.18	0.22	0.89
$D \times S_{ij}$	0.011	0.21	0.23	0.001	0.08	0.002	0.09	0.6	0.37
Sub-canopy									
D_i	0.004	0.002	0.54	0.09	<0.001	0.84	<0.001	0.14	0.93
S_j	0.49	0.86	0.7	0.63	0.06	0.31	0.001	0.62	0.07
$D \times S_{ij}$	0.046	0.015	0.016	0.16	0.29	0.82	0.001	0.9	0.87

Sub-canopy percent basal area by species varied with SDS and BSG (Table 4 and Figure 7). Percent basal areas of jack pine and trembling aspen decreased from exclusion to transition stage for most soil types. The exceptions are that jack pine did not change on medium and moist mineral soils, and aspen did not change on fine soils. Balsam poplar showed no change with SDS. These three species were absent from this layer at the gap stage except for a low percent basal area of trembling aspen on medium soil. While sub-canopy percent basal areas of white birch, white spruce and white cedar did not significantly differ with SDS or BSG, those of black spruce and balsam fir did. Black spruce percent basal area significantly decreased from 60 percent at exclusion to 40 percent at transition to 20 percent at the gap stage on all soils except on moist soils where it increased from transition to exclusion stages and did not change further at the gap stage. Despite the decline from exclusion to transition stage, black spruce had the highest percent basal area of any species. Balsam fir percent basal area increased significantly from exclusion to transition to gap stages (20 percent to 30 percent to 60 percent) for coarse soils and from transition to gap for medium soils. It increased from exclusion to transition for fine and moist soils, but did not differ for fine soils (Figure 7).

Species Importance Value

At the stand level, species importance value varied with SDS and BSG (Figure 8). Pioneer species such as jack pine and trembling aspen clearly dominated the exclusion and transition stages while balsam poplar had much lower importance value. Mid-successional white birch and black spruce had a similar, high importance value at all stages while importance value of late-successional white spruce, balsam fir and white cedar increased with stand development. Among pioneer species at exclusion and transition stages, importance value of jack pine was higher on coarse and medium soils, balsam poplar was higher on medium and moist soils and trembling aspen was greater than 40 percent on all soils except at the exclusion stage on coarse soils. Among mid-successional species, importance value of white birch was higher on coarse, medium and moist soils than on fine soils. Black spruce had the lowest importance value at the

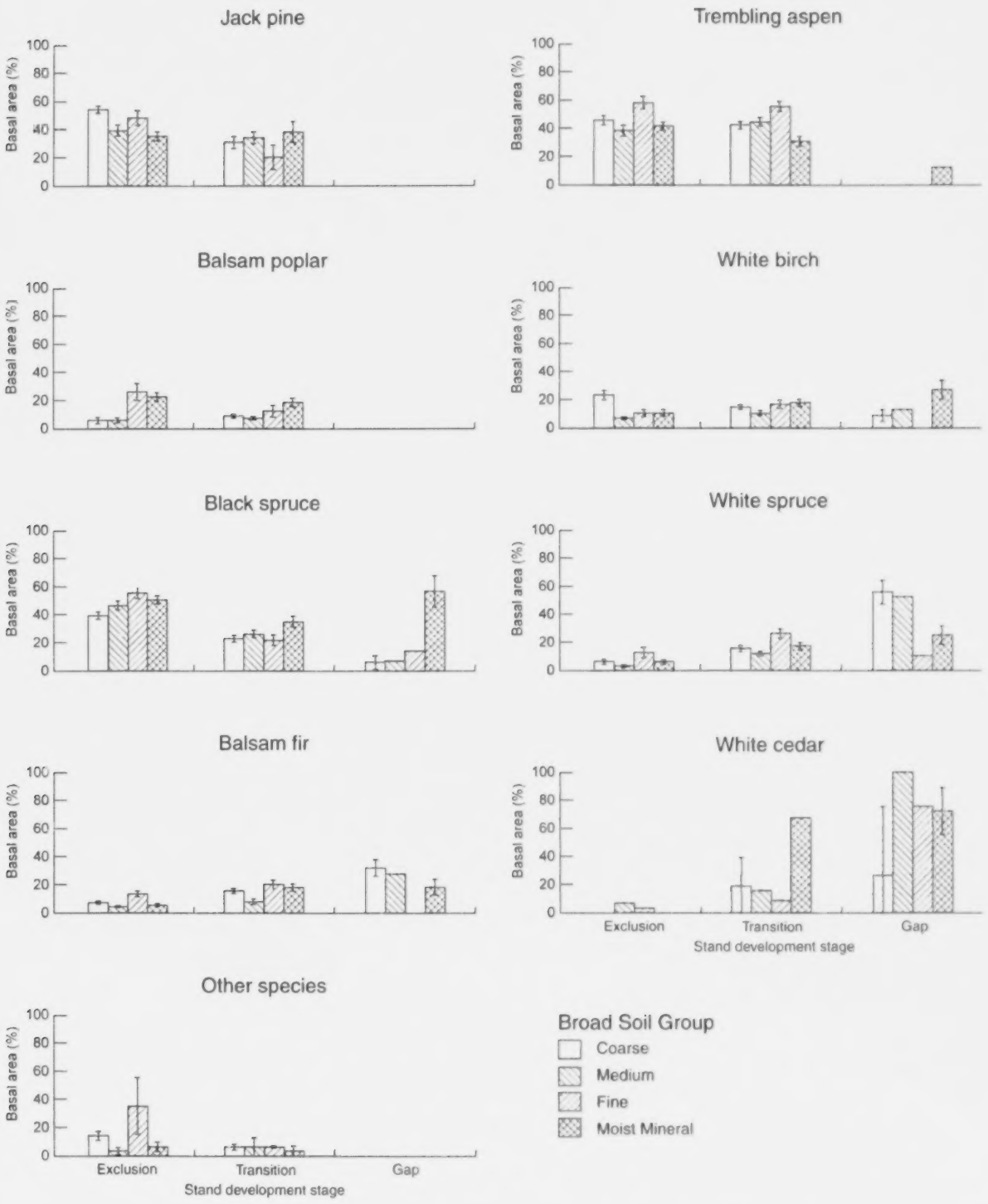

Figure 6. Species-specific percent basal area at stand level in relation to stand development stage and broad soil group.

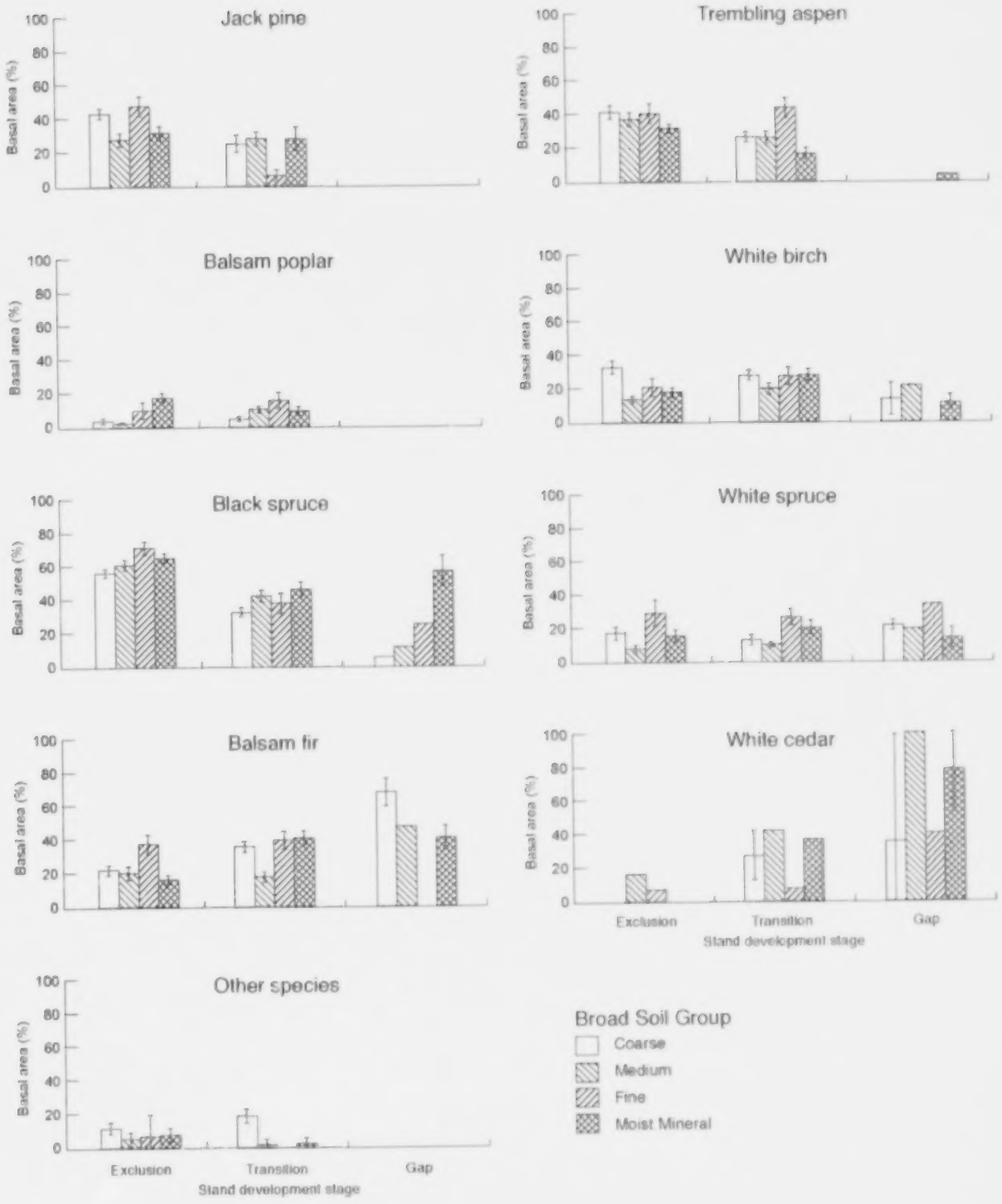

Figure 7. Sub-canopy species-specific percent basal area in relation to stand development stage and broad soil group.

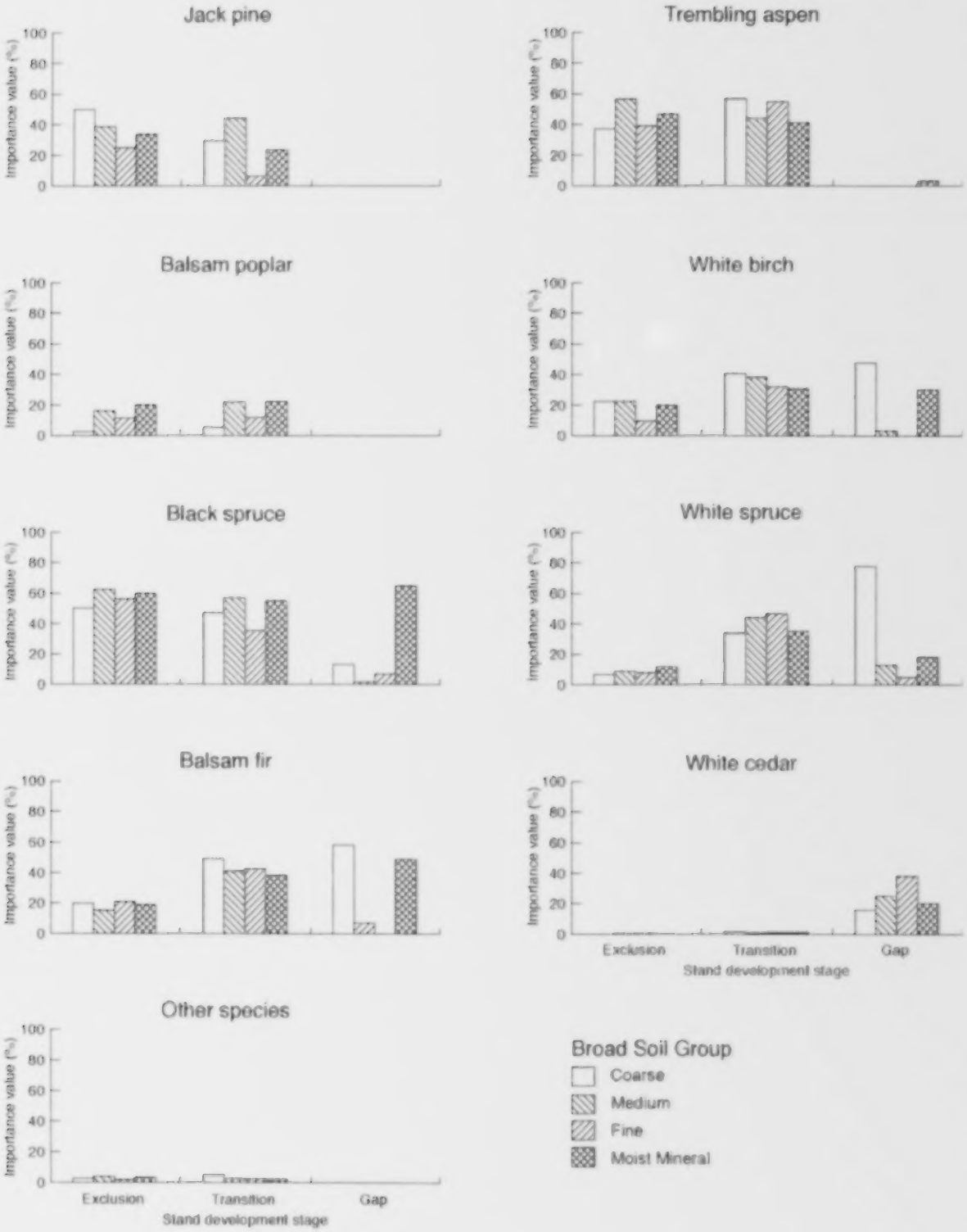

Figure 8. Species importance values at stand level in relation to stand development stage and broad soil group.

gap stage for all soil types except for moist soils. Among late-successional species, balsam fir and white spruce had the highest importance value at the transition stage and at the gap stage on coarse soils. White cedar had its highest importance value at the gap stage.

Sub-canopy importance value for early successional species was lower than for the stand level at all SDSs and on all soils (Figures 8 *vs.* 9). For mid- and late-successional species, almost all sub-canopy species importance value followed the patterns at the stand level (Figures 8 and 9).

Discussion

In boreal mixedwood forests, jack pine, aspen, balsam poplar, white birch and black spruce are common pioneer species that follow a stand-replacing disturbance (Dix and Swan 1971). Black spruce is considered as a pioneer species in some cases (Alexander and Euler 1981, Bergeron *et al.* 1999) and late-successional in other cases (Chen and Popadiouk 2002). Spruce and fir are considered as late successional species because of their frequency in mixedwood stands several decades after disturbance (Dix and Swan 1971, MacDonald and Weingartner 1995). White cedar, a dominant and also an indicator of very old stands, is considered as a late successional boreal mixedwood species (Bergeron 2000).

On Ontario's boreal mixedwood sites, the high frequency (>50 percent) of aspen, jack pine and black spruce confirmed their status as pioneer species characteristic of stands at the exclusion stage. Unexpectedly, aspen and jack pine (typical pioneers) had a lower frequency than black spruce at the exclusion stage on all soils, which may reflect the fact that black spruce is the most frequent species in Ontario's boreal forest. However, these findings may reflect that the databases we used were biased towards black spruce stands, which have been considered economically more important than hardwoods. The high frequency of black spruce in all SDSs (except the gap stage on coarse soils) indicates that black spruce is a poor indicator for identifying SDS.

White birch and late successional species had lower frequencies than pioneer species at the exclusion stage. This strongly suggests that white birch is not a strictly pioneer species like jack pine. White birch frequency at the transition stage was higher than at the exclusion stage, suggesting it either outgrows and outlives its cohorts or enters into a stand after stem exclusion. Such a feature is characteristic of late successional species. Ingress of white birch, similar to spruce, fir and cedar, can be found on rotten wood (Bell 1991), and it can survive in shade for a long time by resprouting (Buell and Niering 1957). White birch stems have been found in stands where they were substantially younger than the time since the last stand-replacing disturbance and were a substantial stand component (Chen and Vasiliauskas, unpublished data). Moreover, the presence of white birch in the gap stage is not unique as it was also documented in old stands in other geographical regions (Frelich and Reich 1995, Bergeron and Harvey 1997, Greene *et al.* 1999, Bergeron 2000).

Pioneer species in the sub-canopy are suppressed individuals of the initial cohort because they usually get established within a few years after disturbance (Ahlgren 1959, Delong 1991, Bélanger *et al.* 1993, Lieffers *et al.* 1996a). This is consistent with our data, as the frequencies of these pioneer species did not significantly differ between exclusion and transition stages on all soils except on coarse soils. Frequencies of the late successional species in the sub-canopy increased significantly from the exclusion to the transition stage, indicating their ingress (Dix and Swan 1971, Lieffers *et al.* 1996a) and a high survival rate in the understory (Comeau *et al.* 1998, Messier *et al.* 1999, Claveau *et al.* 2002) of these shade tolerant species during stand development. White birch is considered a shade intolerant species (Miller 2001), but its frequency trend was similar to white spruce and balsam fir. White birch shade tolerance and resprouting ability have probably been underestimated (Perala and Alm 1990). Black spruce

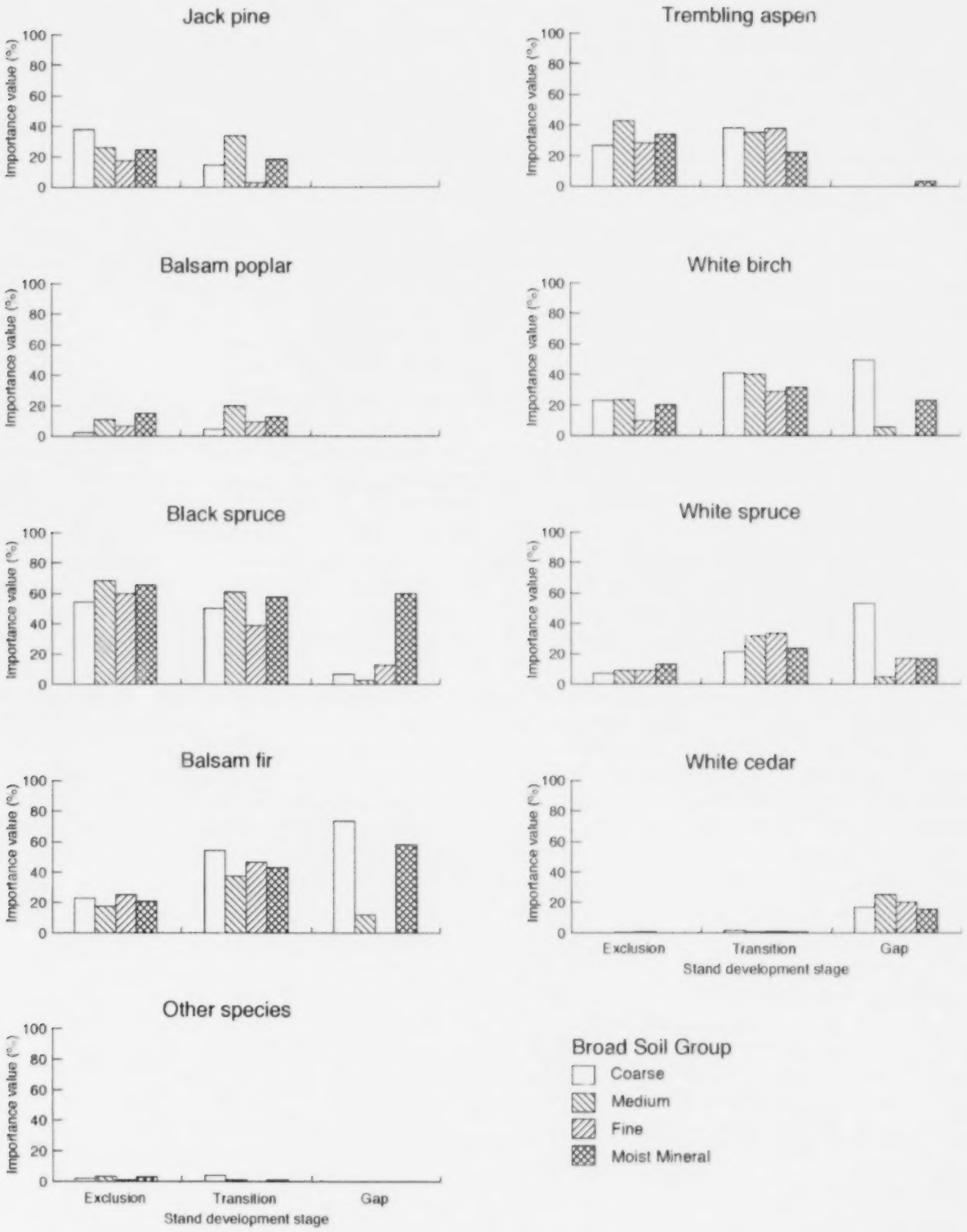

Figure 9. Sub-canopy species importance values in relation to stand development stage and broad soil group.

frequency in the sub-canopy once again demonstrated that this species is successionally neutral and omnipresent on boreal mixedwood sites.

Stand-level changes in percent basal area by species after stand-replacing disturbances has rarely been measured in boreal mixedwood stands (McQuarrie 1975, Day and Bell 1988, Yarie 2000). Ontario's boreal mixedwood definition indicates a compositional shift from pioneer to late successional species (MacDonald and Weingartner 1995). Our data generally supported the conceptual understanding of boreal mixedwood stand development, but found a greater variability in stand composition on boreal mixedwood sites. Pioneers including trembling aspen, jack pine, balsam poplar, white birch and black spruce accounted for the majority of stand basal area at the exclusion stage on all soils. The successional shift towards the transition stage was evident by a decline in percent basal area of pioneer species. The increase in basal area of white birch, along with white spruce and balsam fir, from the exclusion to the transition stage, suggests that white birch bears a characteristic of late successional species. White birch basal area decreased slightly at the gap stage and was replaced by white spruce, balsam fir and white cedar as they became the dominants.

Sub-canopy percent basal areas of pioneer species declined with stand development and the rate of decline differed among BSGs. Trembling aspen did not change on fine soils and jack pine did not decline on medium or moist soils. For late successional species, balsam fir and white cedar increased with stand development. Balsam fir had the highest percent basal area on fine soils. A lack of adequate samples did not allow predictability of balsam fir at the gap stage, but mid- and late-successional stands are favourable for fir if no species-specific damage occurs (Bergeron 2000).

Importance value confirmed our conceptual understanding of boreal mixedwood stand development (Bergeron 2000, Chen and Popadiouk 2002). However, our findings indicate that white birch and black spruce can dominate at various stages of succession compared with the symbolic pathway described by MacDonald and Weingartner (1995). Contrary to Miller (2001), white birch was present at both early and late stages of stand development, indicating that it can colonize canopy gaps caused by non-stand-replacing disturbances. Black spruce can be a pioneer on certain boreal mixedwood sites and a late successional species on other sites (MacDonald and Weingartner 1995). Our findings also indicate that white cedar can be an important component of the last stage of Boreal mixedwoods if not the dominant species, as reported in Quebec (Bergeron 2000).

Stand Density

Stand density varied with SDS and the interaction of SDS and BSG was marginally significant (Table 5). Stand density significantly decreased from exclusion to transition to gap stage on coarse, medium and moist soils, with a more rapid decrease for coarse and medium soils compared with moist soils. Density was low and did not differ among SDSs on fine soils. (Figure 10). Similar to total stand density, canopy and sub-canopy density significantly decreased with stand development on coarse, medium and moist soils (Table 5 and Figures 10A and C), with no change on fine soils.

Stand density at the exclusion and transition stages was similar to stand density of early successional boreal mixedwood species from Plonski (1974). The dynamic process of reduction in density that we found is consistent with the understanding of stand development (Oliver and Larson 1996, Chen and Popadiouk 2002). However, species-specific densities in response to SDS may need to be further examined to address the coupling of compositional changes and density reductions associated with stand development.

Table 5. P-values from analysis of variance for stand, canopy and sub-canopy density (stems/ha) by stand development stage (D_i) and broad soil group (S_j).

Source	Stand	Canopy	Sub-canopy
D_i	0.001	0.001	0.01
S_j	0.42	0.25	0.69
$D \times S_{ij}$	0.06	0.06	0.04

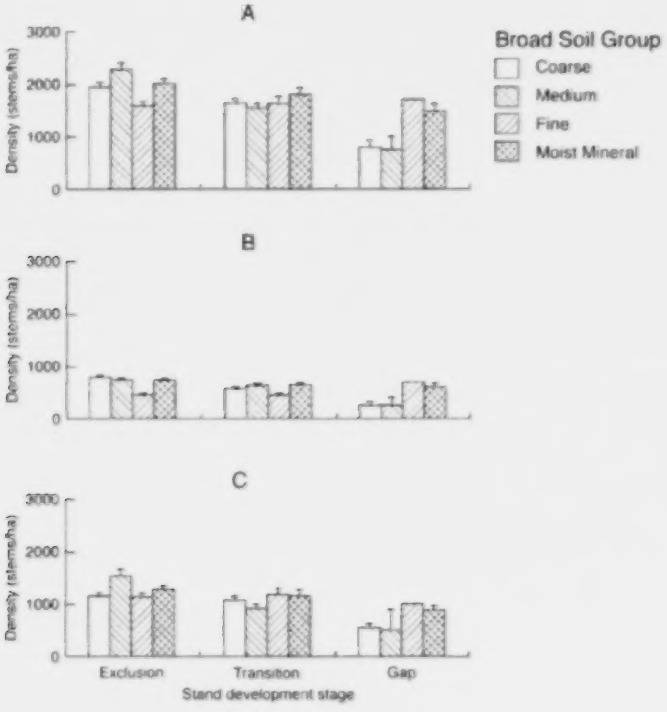

Figure 10. Density in relation to stand development stage and broad soil group for: A) stand, B) canopy and C) sub-canopy.

Sapling and Seedling Frequency and Density

Results

Sapling Frequency and Density

Four hundred and sixty-four plots were used to analyse sapling percent cover by species (Appendix 1), and 283 plots were used to analyse sapling densities. Sapling frequency was calculated using all 747 plots. Sapling species were the same as for the overstory with the addition of black asn, mountain ash (*Sorbus* spp. L.), tamarack and red maple.

Sapling frequency varied with species (Figure 11). Of the three early-successional species, jack pine and balsam poplar frequencies were very low while trembling aspen frequency varied

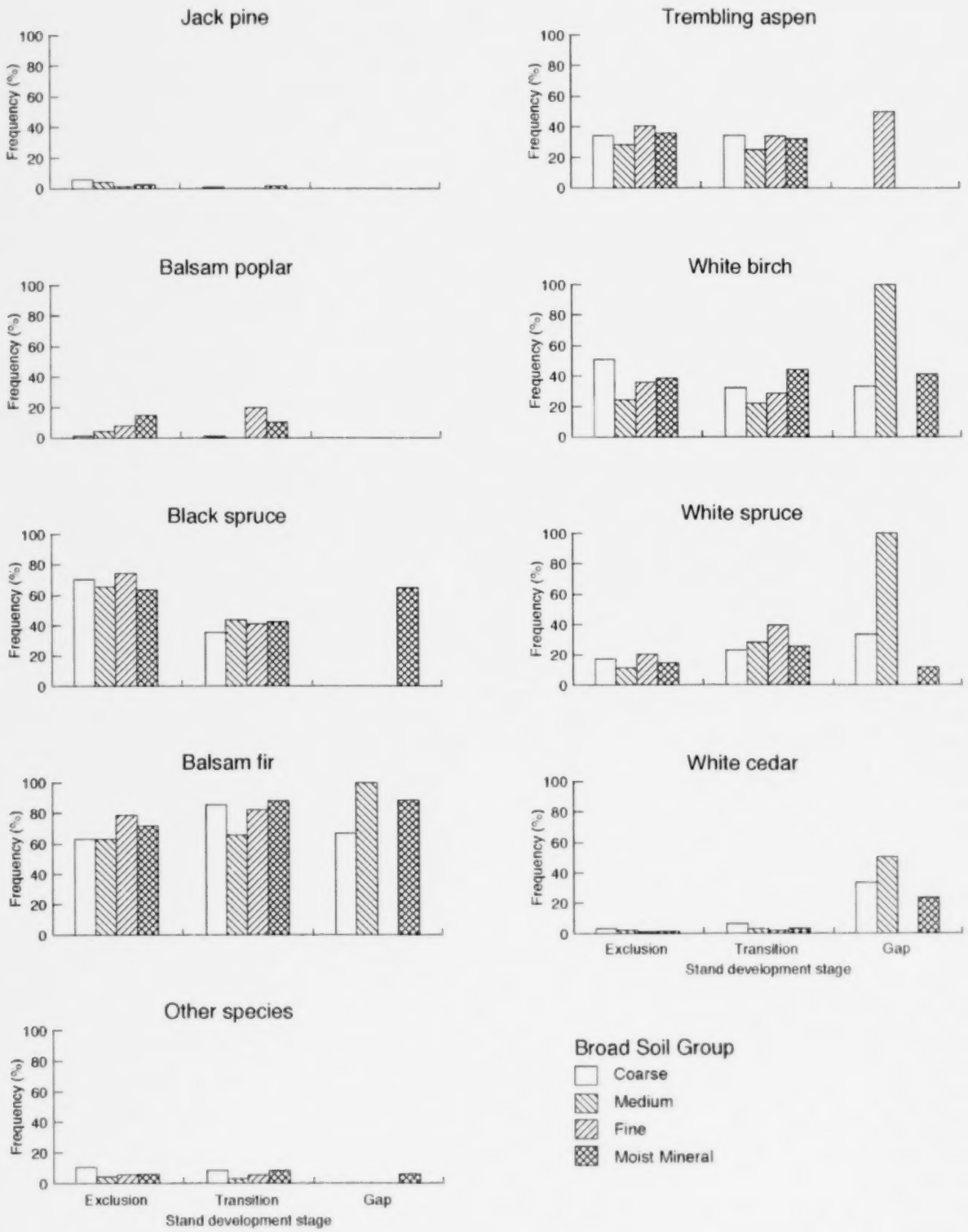

Figure 11. Species-specific sapling frequency in relation to stand development stage and broad soil group.

between 30 to 60 percent among SDSs and BSGs. White birch and black spruce had higher frequencies than pioneers, ranging from 25 to 100 percent for white birch and 40 to 75 percent for black spruce. Among late-successional species, balsam fir frequency ranged from 60 to 100 percent, white spruce frequency from 15 to 100 percent while white cedar was infrequent until the gap stage (Figure 11).

Total sapling density ranged from 600 to 1400 stems/ha with a significantly lower density at the transition stage on medium soils (Table 6 and Figure 12). Species-specific sapling density did not significantly differ among SDSs or BSGs except for black spruce and balsam fir (Table 6). Black spruce sapling density significantly decreased from exclusion to transition to gap stages on all soils (Table 6 and Figure 13). Balsam fir had the highest sapling density of all species. Its density increased from the exclusion to the transition stage and was generally higher on fine and moist soils than on coarse and medium soils.

Table 6. P-values from analysis of variance for total sapling and species-specific sapling density (stems/ha) by stand development stage (D_i) and broad soil group (S_j).

Source*	Total	Jack pine	Aspen	Balsam poplar	White birch	Black spruce	White spruce	Balsam fir	White cedar	Other species
D_i	0.39	0.76	0.18	0.87	0.52	<0.001	0.09	0.14	0.77	0.88
S_j	0.43	0.97	0.98	0.64	0.23	0.46	0.93	0.18	0.92	0.97
D x S_{ij}	0.03	0.96	0.62	0.95	0.63	0.13	0.14	0.04	0.74	0.88

*Note: Values for total and species-specific densities were square-root transformed.

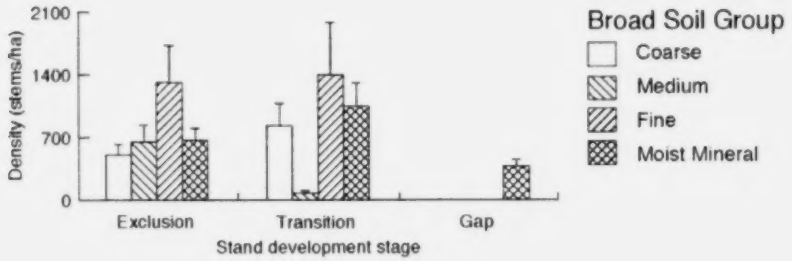

Figure 12. Sapling density in relation to stand development stage and broad soil group.

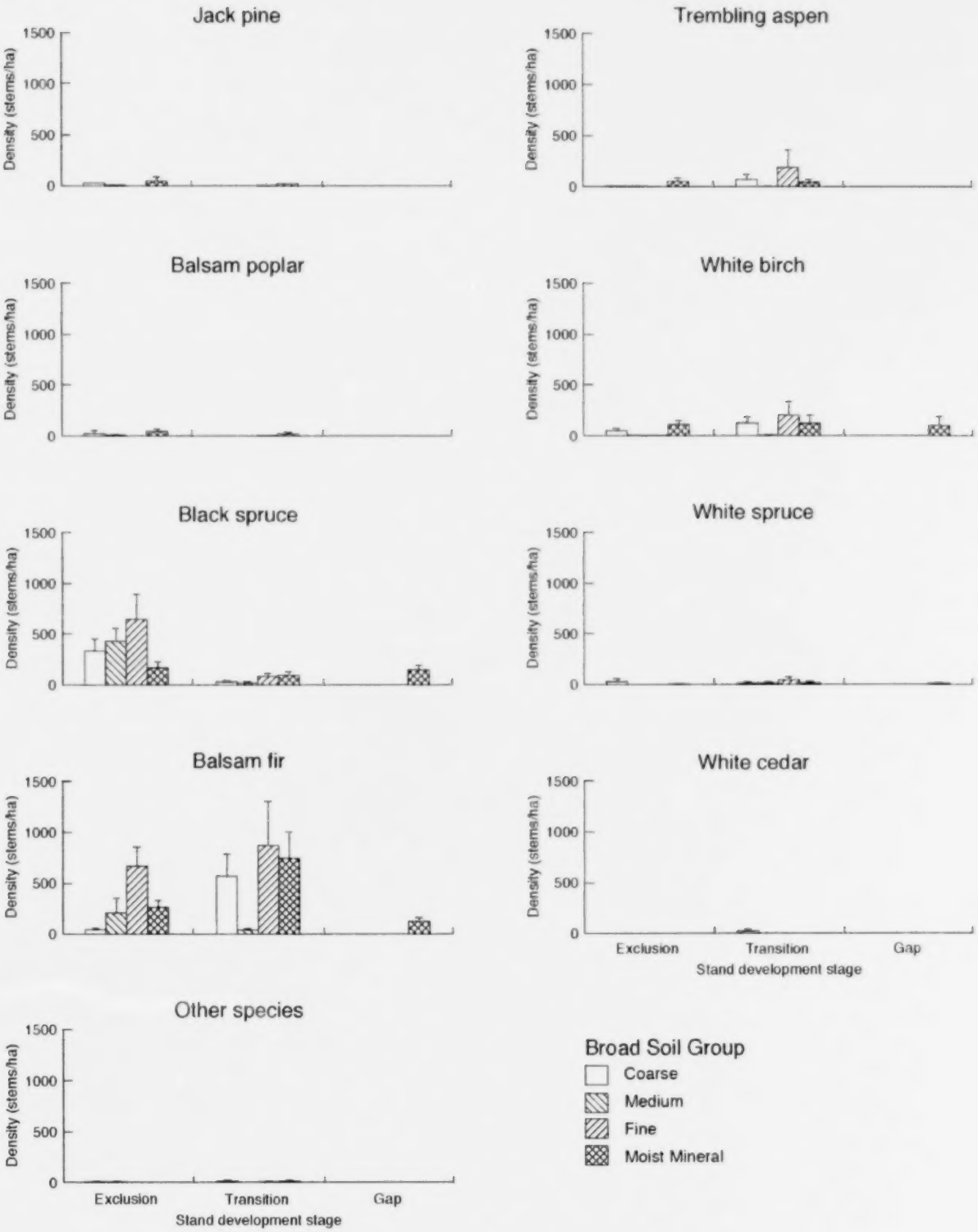

Figure 13. Species-specific sapling density in relation to stand development stage and broad soil group.

Seedling Frequency and Density

Seedlings were surveyed in only 88 G&Y plots (Appendix 1). Similar to sapling frequency, seedling frequency also significantly varied with SDS and BSG ($P < 0.05$). Jack pine seedling frequency was low for all stages on all soils (Figure 14). Trembling aspen and balsam poplar had much higher frequencies than expected for shade intolerant species, going up to 70 percent for aspen at the transition stage on medium soils (Figure 14). Among the mid- and late-successional species, balsam fir had the highest frequency at all stages on all soils, followed by white birch, black spruce and white spruce. Their frequencies generally increased with stand development except for black spruce, which decreased on coarse soils (Figure 14). White cedar seedling frequency was low on all soils.

Mean total seedling density varied from 100 to 6000 stems/hectares (Table 7 and Figure 15). Balsam fir was the only species with a significant increase in seedling density with stand development (Table 7), and accounted for the majority of seedlings. White spruce had a high seedling density, over 1200 stems/ha, at the exclusion stage on coarse soil, and was much lower or absent on other soils and stages (Table 7 and Figure 16). Trembling aspen had low seedling densities, but was present at the exclusion and transition stages on all soils. Densities of all other species were very low.

Discussion

Understory saplings and seedlings can represent small trees from the same cohort as the overstory or a new cohort through stand development. The stem exclusion stage does not favour the establishment of new trees (Oliver and Larson 1996), however, Chen and Popadiouk (2002) defined the boreal mixedwood stem exclusion stage in such a way that it includes the early stage of understory re-initiation of Oliver and Larson (1996). Black spruce and balsam fir were very common in the understory at the stem exclusion stage for all soils. Even trembling aspen, which usually occurs in large gaps (Leemans 1991, Qinghong and Hytteborn 1991), had a high frequency at the stem exclusion stage. Closed canopies do not favour growth of any seedlings (Claveau *et al.* 2002), but even shade intolerant species could survive several years under 10 percent of full sunlight (Messier *et al.* 1999). The high frequency of aspen in the understory may be due to frequent forest tent caterpillar (*Malacosoma disstria* Hbn.) defoliations in Ontario's boreal mixedwoods, which result in a reduced amount of auxin reaching the roots. Auxin is a plant hormone that controls apical dominance, and the reduction in auxin along with warmer soil temperatures promotes aspen suckering in forest understories (Perala 1990). As the epidemic ends and full shading is restored to these stands, the suckers may gradually die out and disappear. The increase in frequency of balsam fir and white spruce with stand development was expected because of their shade-tolerance (Dix and Swan 1971, Messier *et al.* 1999), but the decreasing frequency of black spruce on either coarse or fine soils was not expected because of its late successional status (MacDonald and Weingartner 1995). White cedar saplings were more frequent at the gap stage, indicating its late successional status and presence on sites with long fire return intervals (Bergeron *et al.* 1998).

Sapling and seedling densities for black spruce reported here are lower than those on black spruce dominated upland sites (Arnup 1996). Balsam fir seedling densities are higher on boreal mixedwood sites than those reported by Arnup (1996). Inherent differences in site conditions and overstory cover between upland black spruce stands and boreal mixedwoods may explain the difference in advance regeneration densities. The greater shrub coverage found on richer boreal mixedwood sites could negatively affect sapling and seedling establishment (OMNR 1997). Advance regeneration cannot be reliably predicted from SDS and BSG. This justifies the need for a pre-harvest assessment when developing a silvicultural prescription for an

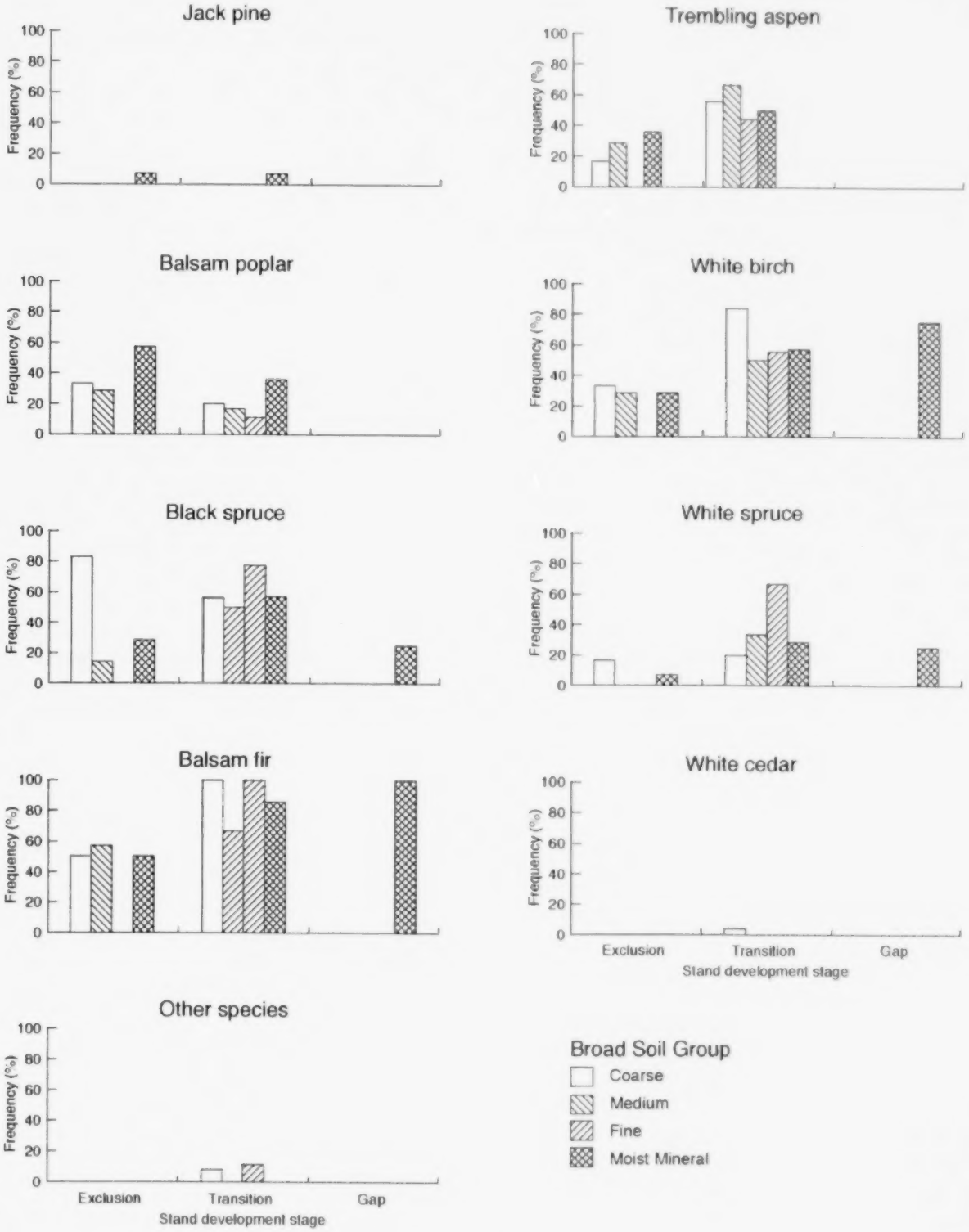

Figure 14. Species-specific seedling frequency in relation to stand development stage and broad soil group.

Table 7. P-values from analysis of variance for total seedling and species-specific seedling density (stems/ha) by stand development stage (D_i) and broad soil group (S_j).

Source*	Seedling total	Jack pine	Aspen	Balsam poplar	White birch	Black spruce	White spruce	Balsam fir	White cedar	Other
D_i	0.07	0.73	0.46	0.41	0.17	0.77	0.93	0.04	0.93	0.84
S_j	0.86	0.91	0.31	0.85	0.58	0.92	0.06	0.41	0.96	0.86
$D \times S_{ij}$	0.5	0.89	0.61	0.84	0.93	0.97	0.22	0.71	0.99	0.92

*Note: values for total and species-specific densities were square-root transformed.

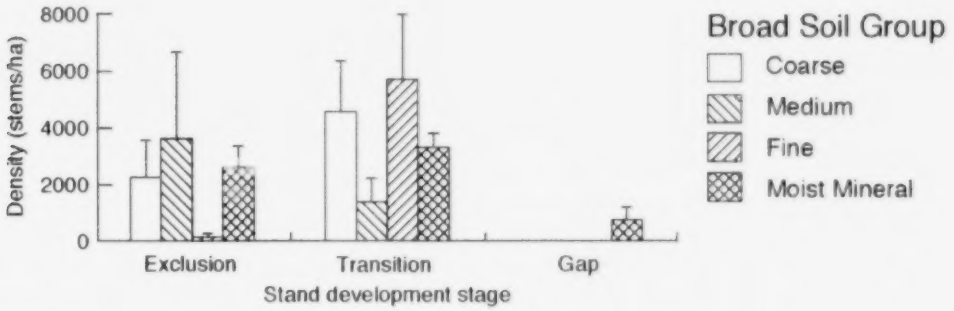

Figure 15. Seedling stem density in relation to stand development stage and broad soil group.

Ontario boreal mixedwood site (OMNR 2003), in particular when advance growth is used as the main means of achieving regeneration objectives for future stands.

Shrubs and Non-woody Vegetation

Results

Frequency

Shrubs occurred on almost all plots at all stages and soil types (Figure 17). Frequencies of tall, medium and low shrubs varied significantly with SDS and BSG ($P < 0.05$). Tall shrub frequency increased from exclusion to transition to gap stage on all soils, except from transition to gap stage on moist soils where its frequency stayed high (Figure 17). Medium shrubs occurred with a nearly 100 percent frequency at all stages and soil types (Figure 17). Low shrub frequency decreased with SDS on coarse and medium soils, but did not change on other soils and it was highest on moist soils for all SDSs (Figure 17).

Herbs had a 100 percent frequency for all stages and soil types (Figure 17). Frequency of grasses and sedges increased from the exclusion to the transition stages on all soils and further increased to the gap stage on coarse and fine soils. It was also significantly higher on fine and moist than on coarse and medium soils (Figure 17). Mosses, like herbs, were present in

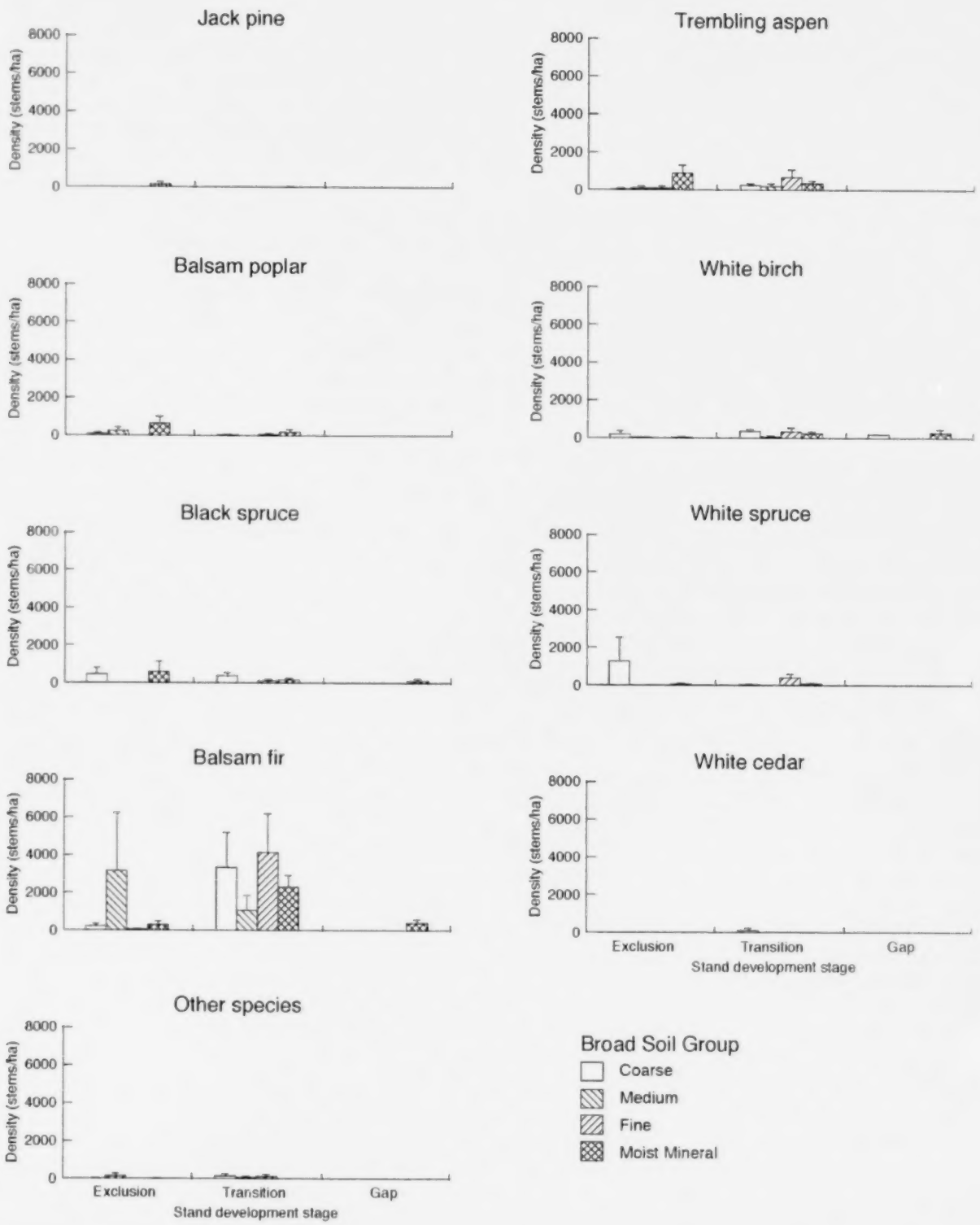

Figure 16. Species-specific seedling density in relation to stand development stage and broad soil group.

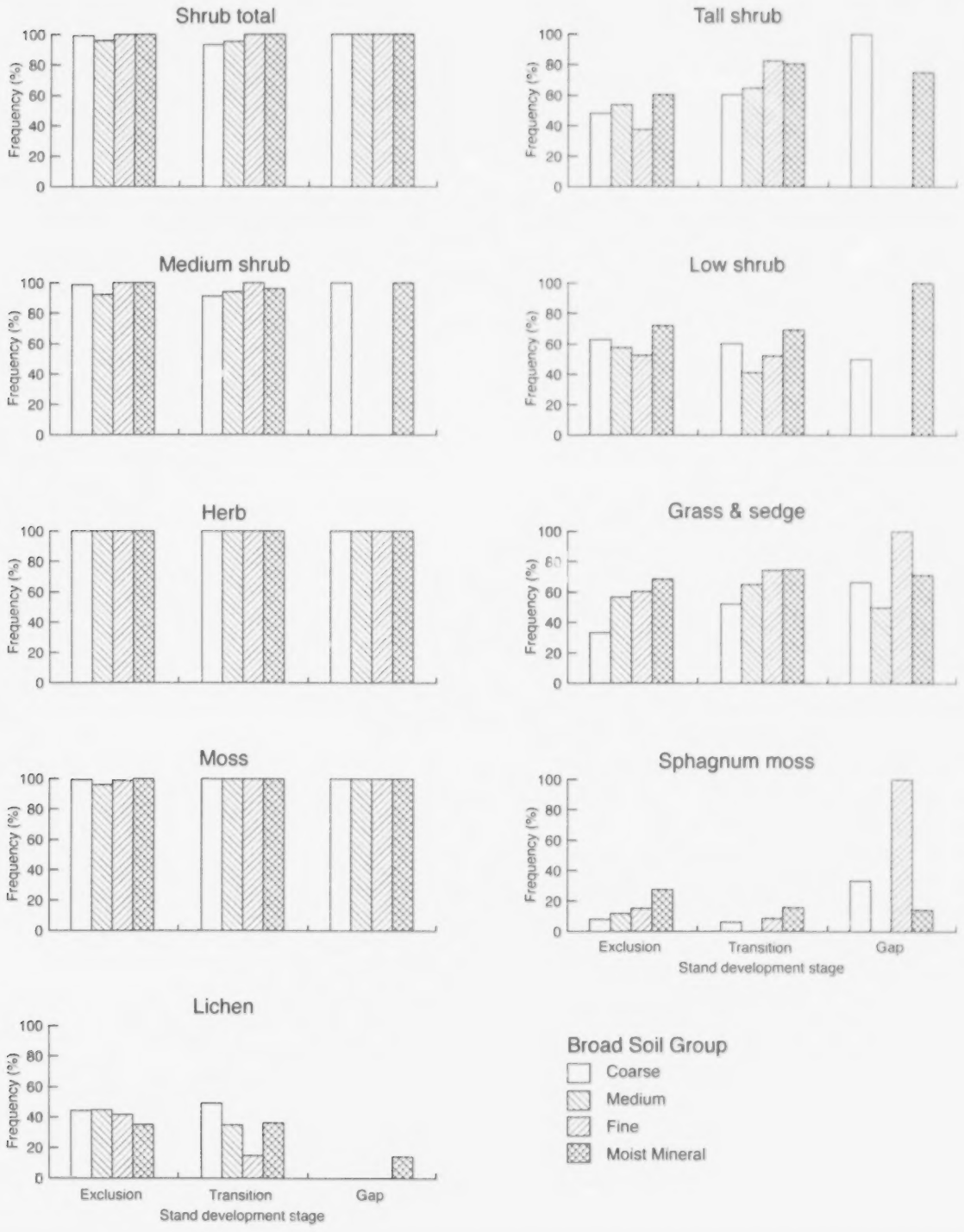

Figure 17. Frequency of shrubs and non-woody vegetation in relation to stand development stage and broad soil group.

almost all plots with the lowest frequency (96 percent) for medium soils at the exclusion stage. *Sphagnum* moss frequency was significantly higher on fine and moist soils than on coarse and medium soils at the exclusion and transition stages while its highest frequency occurred at the gap stage on fine soils (Figure 17). Lichen frequency generally decreased with stand development and it was higher on coarse and medium soils than on fine and moist soils.

Among all shrubs and non-woody species, the following species were analyzed separately because of their competitiveness on boreal mixedwood sites: green alder (*Alnus crispa* (Ait.) Turrill), speckled alder, beaked hazel, bush honeysuckle (*Diervilla lonicera* Mill.), prickly wild rose (*Rosa acicularis* Lindl.), mountain ash, wild red raspberry (*Rubus idaeus* var. *strigosus* (Michx.) Maxim.), Labrador tea (*Ledum groenlandicum* Oeder) and large-leaved aster (*Aster macrophyllus* L.). Other potential competitors including blue-joint grass (*Calamagrostis canadensis* (Michx.) Beauv.), red maple, mountain maple, pin cherry (*Prunus pensylvanica* L.f.) and thimbleberry (*R. parviflorus* Nutt.) were found infrequently on Ontario's boreal mixedwood sites (i.e. frequency <20 percent).

Among these species, speckled alder, beaked hazel, bush honeysuckle, prickly wild rose and large-leaved aster had highest frequencies (Figure 18). Frequencies of speckled alder, beaked hazel and large-leaved aster increased with SDS on coarse, medium and fine soils while the frequencies of speckled alder and beaked hazel decreased with SDS on moist soils. At the exclusion and transition stages, bush honeysuckle was more frequent on coarse and medium soils and prickly wild rose was more frequent on fine and moist soils. Frequencies for both species declined at the gap stage and both species were also absent from fine and medium soils. Of the less frequent species, mountain ash and green alder were most frequent on coarse and medium soils. Mountain ash was absent at the gap stage on medium soils. Wild red raspberry was most frequent at the exclusion and transition stages on moist soils and at the gap stage on coarse soils. Labrador tea was more frequent at the stem exclusion stage than at the gap dynamics stage.

Cover

Total percent cover of shrubs did not differ among SDSs or BSGs. Non-woody vegetation differed only among SDSs with a lower percent cover at the transition stage (Table 8 and Figure 19). Percent cover of tall shrubs was significantly higher on moist soils at the gap stage. (Table 8 and Figure 20). Medium shrub cover did not vary significantly among BSGs but was significantly higher at the gap stage. Low shrub percent cover significantly increased with stand development and peaked at the gap stage on moist soils.

Of non-woody vegetation, herbs and mosses had higher percent cover than grasses and sedges, *Sphagnum* mosses and lichens (Figure 20). Herb, grass and sedge, and *Sphagnum* moss cover did not change significantly with SDS or BSG (Table 8 and Figure 20). Moss cover significantly differed among SDSs (Table 8) with the lowest cover at the transition stage (Figure 20). Lichen percent cover decreased significantly with stand development (Figure 20).

Cover of selected shrubs and herbs did not vary significantly between SDSs or BSGs (Table 9). Among these species, large-leaved aster had the highest percent cover, followed by beaked hazel, bush honeysuckle, speckled alder, Labrador tea, green alder, prickly wild rose, wild red raspberry and mountain ash (Figure 21).

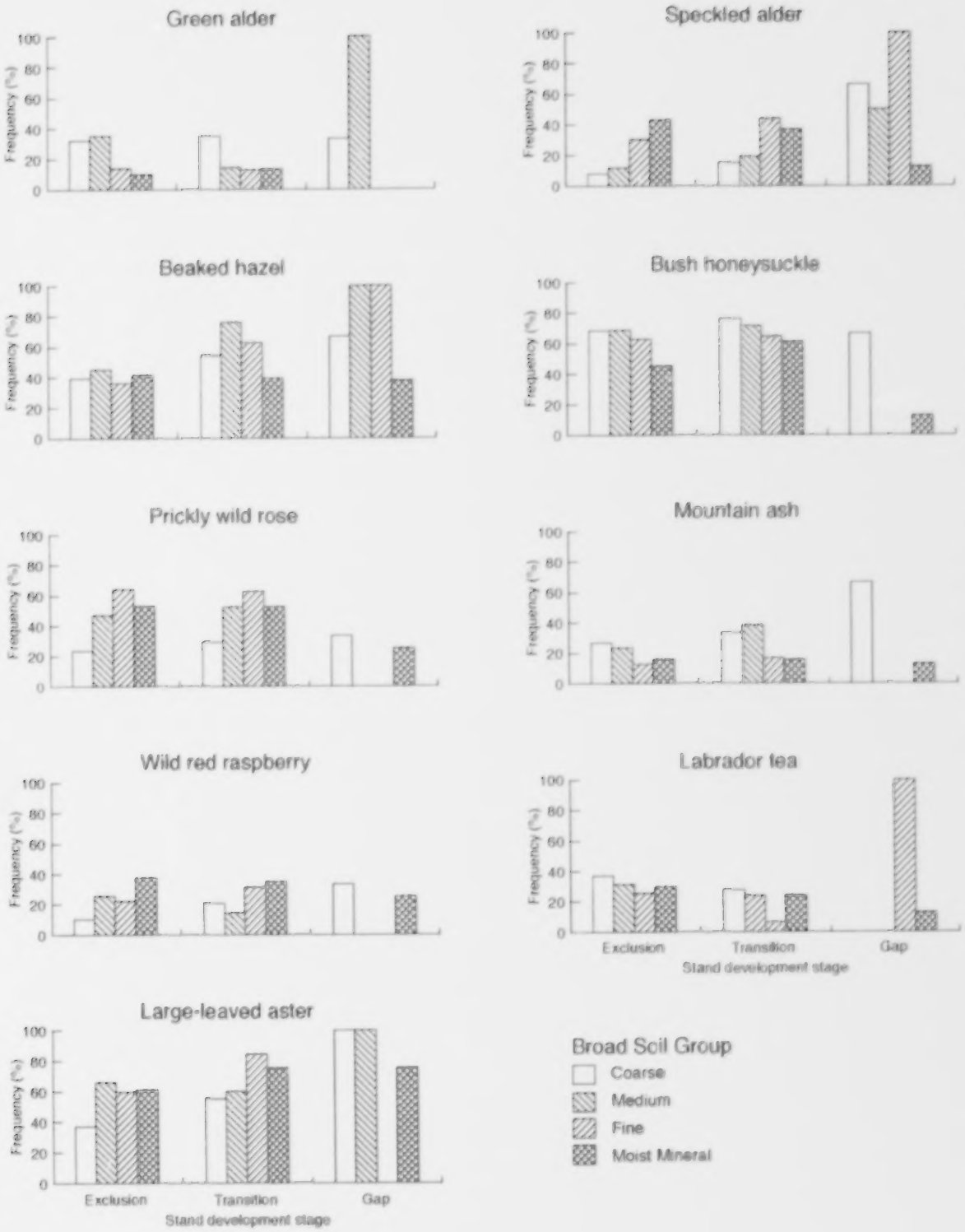

Figure 18. Selected shrub and non-woody species frequency in relation to stand development stage and broad soil group.

Table 8. P-values from analysis of variance of shrub and non-woody vegetation percent cover by stand development stage (D_i) and broad soil group (S_j).

Source	Shrub				Non-woody vegetation					
	Total	Tall	Medium	Low	Total	Herbs	Grasses & Sedges	Moss	Sphagnum	Lichen
D_i	0.60	0.89	0.01	0.04	0.001	0.39	0.49	<0.001	0.99	0.050
S_j	0.40	0.008	0.43	0.02	0.57	0.43	0.99	0.57	0.90	0.85
$D \times S_{ij}$	0.46	0.052	0.22	0.33	0.36	0.16	0.47	0.23	0.97	0.66

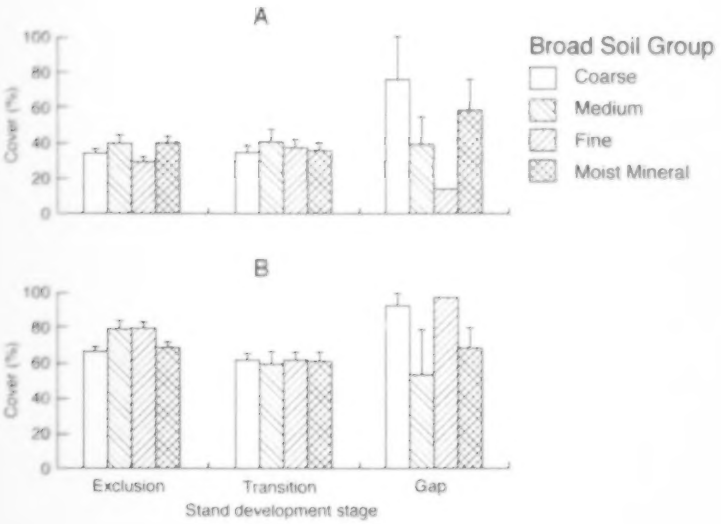

Figure 19. Percent cover of shrub (A) and non-woody vegetation (B).

Table 9. P-values from analysis of variance of percent cover of selected species by stand development stage (D_i) and broad soil group (S_j).

Source	Green alder	Speckled alder	Beaked hazel	Bush honeysuckle	Prickly wild rose	Mountain ash	Wild red raspberry	Labrador tea	Large-leaved aster
D_i	0.27	0.31	0.83	0.96	0.21	0.84	0.69	0.38	0.60
S_j	0.90	0.80	0.84	0.45	0.82	0.052	0.29	0.53	0.37
$D \times S_{ij}$	0.23	0.83	0.96	0.99	0.44	0.58	0.98	0.97	0.11

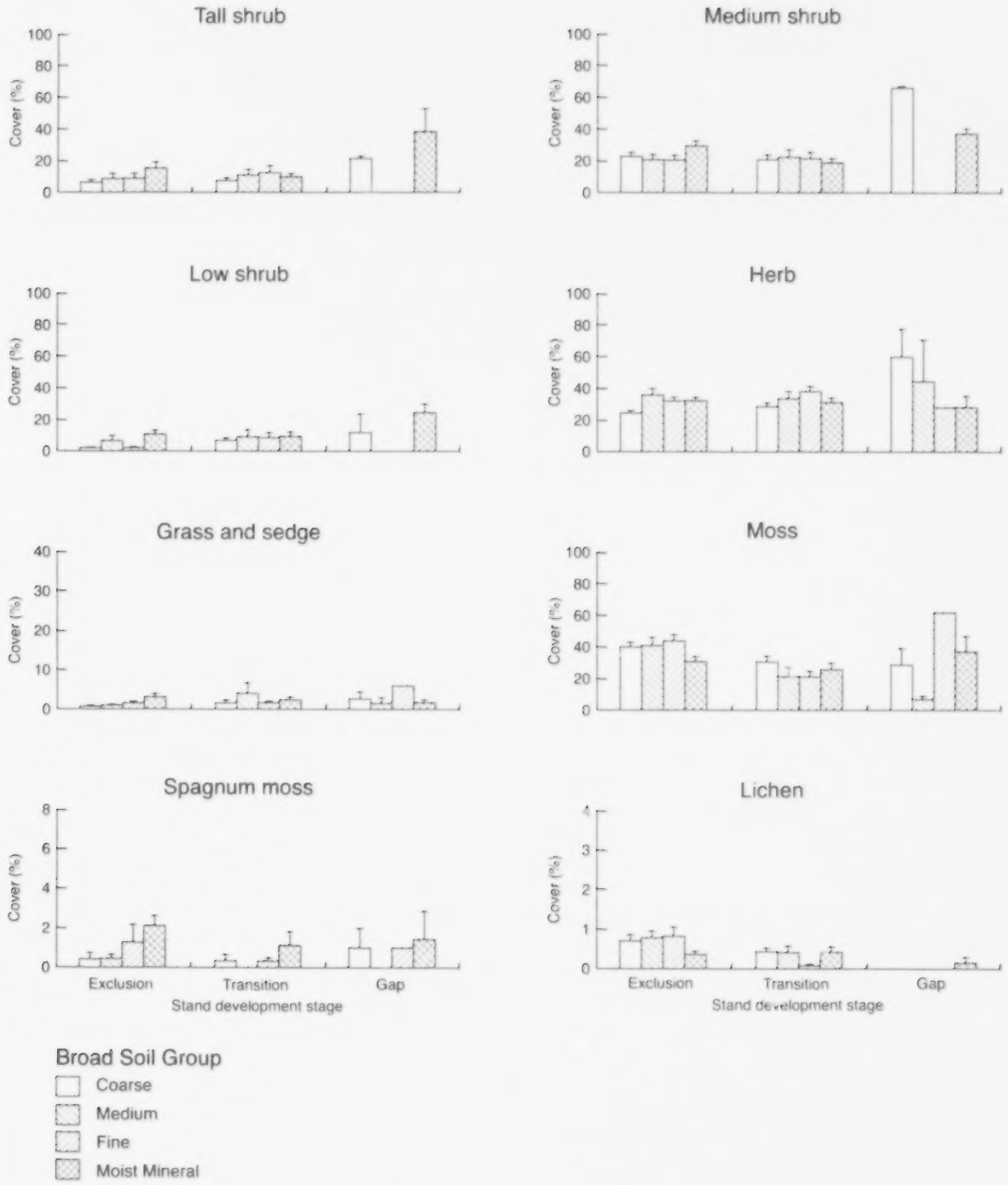

Figure 20. Group-specific percent cover of shrub and non-woody vegetation in relation to stand development stage and broad soil group.

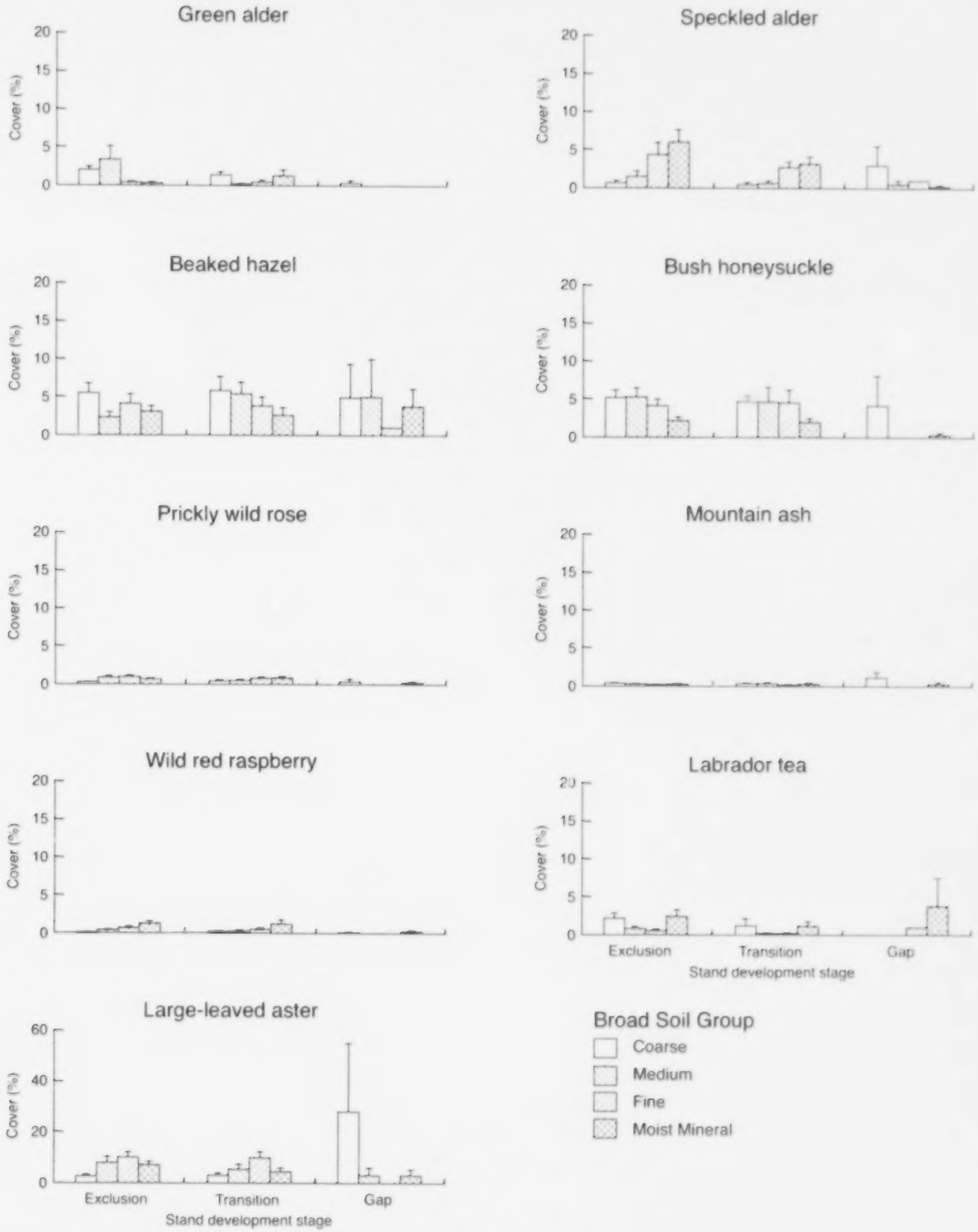

Figure 21. Species-specific percent cover of selected shrub and non-woody species in relation to stand development stage and broad soil group.

Importance Value

Tall shrubs importance value increased with stand development (Figure 22). Medium shrubs had the highest importance value among the three shrub layers. Importance value for medium shrubs peaked on coarse soils at the gap stage. Low shrubs had the lowest importance value for any shrub layer (Figure 22), and had the highest importance value at the gap stage on moist soils (Figure 22). Herbs and mosses had the highest importance value for non-woody vegetation, ranging from 55 to 80 percent. Importance value for grasses and sedges was higher on fine and moist soils than on coarse and medium soils with the highest importance value at the gap stage on fine soils. Importance value for *Sphagnum* mosses and lichens was generally low except that *Sphagnum* moss importance value increased to 50 percent at the gap stage on fine soils (Figure 22).

Among the selected species, speckled alder, beaked hazel, bush honeysuckle, prickly wild rose and large-leaved aster generally had higher importance value than green alder, mountain ash, wild red raspberry and Labrador tea (Figure 23). Speckled alder importance value increased with stand development except on moist soils where it decreased and was generally higher on fine and moist soils. Beaked hazel importance value increased with stand development on coarse, medium and fine soils and decreased for moist mineral soils. Importance value for large-leaved aster also increased with stand development for all soils, while importance value for bush honeysuckle increased from exclusion to transition and then decreased at the gap stage and was also lower on fine and moist soils. Prickly wild rose importance value was lower on coarse soils and higher on fine and moist soils with lower value found at the gap stage.

Discussion

Shrubs and non-woody vegetation are important components of boreal forests at any SDS as they can establish and grow on all soils under various light conditions (Kurmis and Sucoff 1989, Arnup *et al.*1995, Helm and Collins 1997, Qi and Scarratt 1998). Our data indicated the ubiquitous nature of shrubs and non-woody vegetation on Ontario's boreal mixedwood sites. Although some species may be scarce because of deep shade (Messier 1996, Aubin *et al.* 2000). Over 40 species with different morphological and ecological traits were included in the total shrub cover. Such a heterogeneous group can react differently to individual sites, with the result that total shrub cover did not significantly change with SDS or BSG.

Some trends became apparent after splitting shrubs into three size classes. Importance value of tall and medium shrubs increased at the gap stage with a greater increase on coarse than moist soils. On moist soils, low shrubs were more important than on other soils, especially at the gap stage. Dense shrub foliage can suppress growth of small trees and cause excessive mortality of crop species (Lieffers *et al.* 1996b, DeLong *et al.* 1997). The increase in cover of tall and medium shrubs coincided with a decrease in sapling and seedling densities on moist soils at the gap stage (Figures 12 and 15).

Non-woody vegetation percent cover was twice that of shrubs at the exclusion and transition stages on all soils (Figure 19). Mosses (other than *Sphagnum* spp.) and herbs were both most frequent and had the highest percent cover of any component of the ground vegetation on all soils. At the transition stage, moss cover on medium and fine soils was relatively low (25 percent), nonetheless, much greater than in the mixedwood forest in western Quebec (three percent) (DeGrandpré *et al.* 1993). A significant decrease in moss cover from the exclusion to the transition stage does not support the assumption that mosses survive better than other plants underneath shade-tolerant conifers (Payette *et al.* 2000, Yarie 2000), where hardwoods were absent or only a minor component. The high herbaceous cover on boreal mixedwood

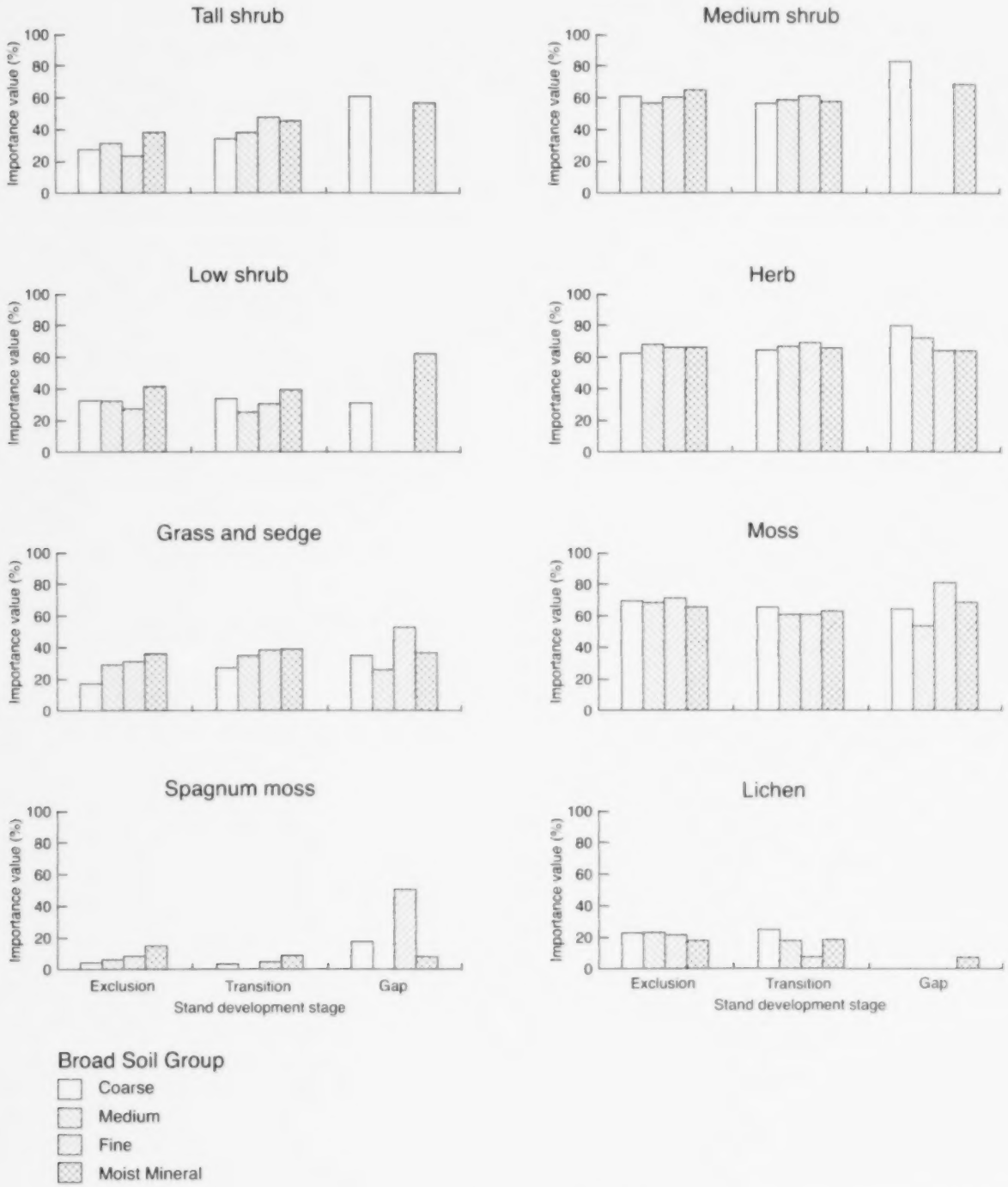

Figure 22. Importance value of shrubs and non-woody vegetation in relation to stand development stage and broad soil group.

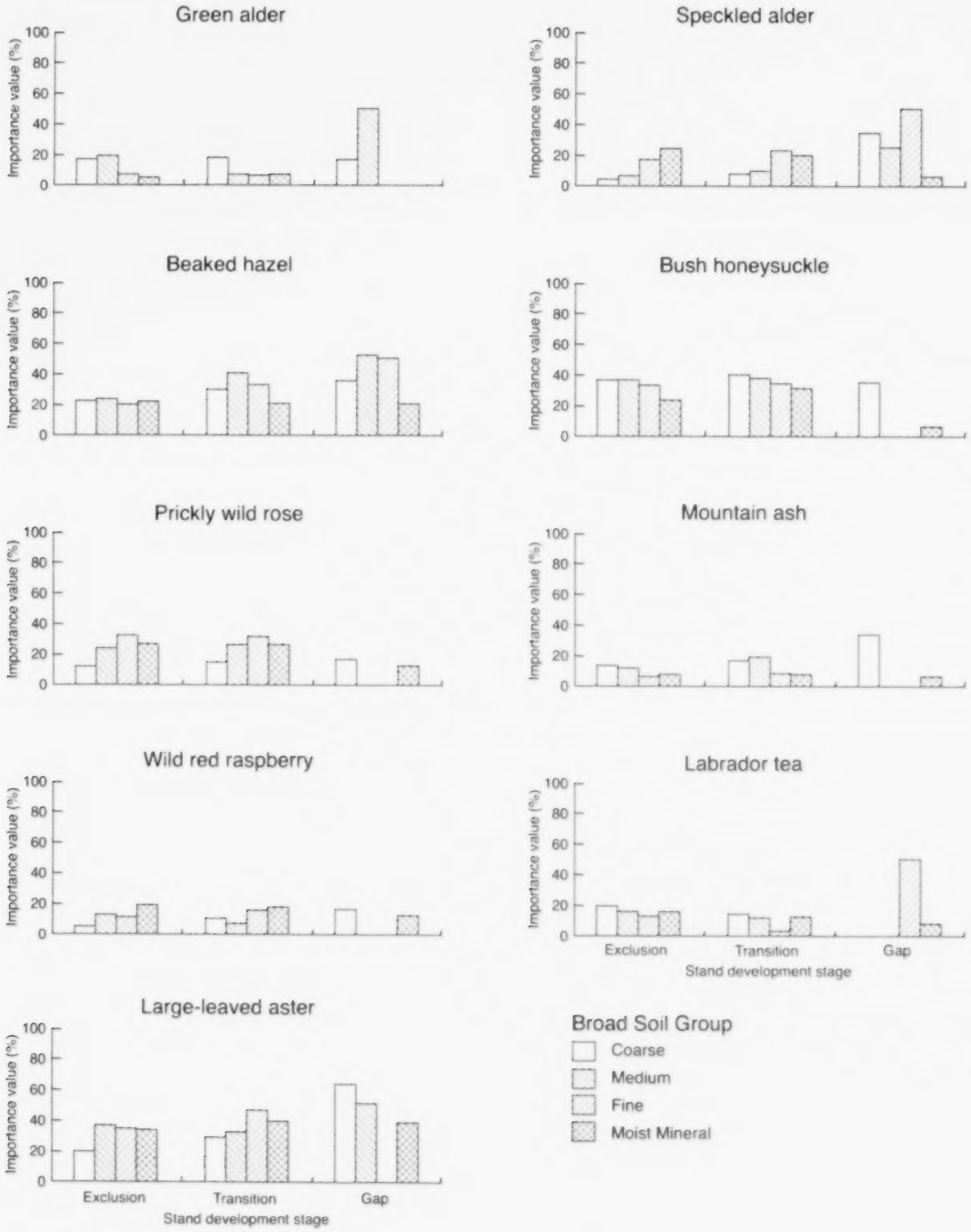

Figure 23. Importance value of selected shrub and non-woody species in relation to stand development stage and broad soil group.

sites may be important in reducing moss abundance. Competition from grasses, *Sphagnum*, or lichens was less likely as their percent cover was generally low. The chemical composition and physical structure of litter (including coarse woody debris) may also influence moss cover (Saetre *et al.* 1997). The more fertile soils on boreal mixedwood sites might have promoted herb and shrub growth over mosses.

The vascular flora of the boreal forest numbers well over 1000 species (La Roi 1967). The majority of these species do not cause problems for regeneration of crop trees, but some do (Wedeles *et al.* 1995, Bell *et al.* 2000). Shrubs, especially tall shrubs, are the primary competitors for seedlings and saplings (Kirby 1962, Greene *et al.* 1999, Bell *et al.* 2000). Our selected species did not individually have a high percent cover, as none of them covered more than 20 percent. Bush honeysuckle and prickly wild rose were more important at the exclusion stage, speckled alder and beaked hazel at the gap stage, while large-leaved aster was important through all SDSs. The very low frequency and abundance of some species does not necessarily mean that they also have a low importance at the stand initiation stage. Species such as Canada blue-joint and raspberry can rapidly colonize a disturbed area through soil seed banks, dormant rhizomes, or long-distance seed dispersal (Peterson *et al.* 1989, Messier 1996). Because of their presence in mature stands, most of the selected species can readily expand their cover after a stand-replacing disturbance.

Organic Horizons

Depth of organic horizons varied significantly with SDS and BSG (Table 10 and Figure 24). Depth of total organic layer (L-, F- and H-horizons) was lower at the transition stage and significantly greater at the exclusion and gap stages on coarse and moist soils while there was no difference among SDSs on medium and fine soils. Depth of H-horizon was greater at the gap stage than other stages and it was greatest on moist soils while that of L- and F-horizons did not change between SDSs or BSGs.

Humus form frequencies varied significantly with SDS and BSG ($P < 0.001$). Mors were the dominant humus form, followed by moders and mulls which were very infrequent. Mulls occurred at the exclusion stage on fine and moist soils and at the transition stage on all soils, but did not occur at the gap stage (Figure 25). Mors were highly frequent at the exclusion and transition stages. The limited number of sample plots at the gap stage, however, precluded a conclusion for the relationship between humus form frequency and BSG.

The cold climate of the boreal forest does not favour fast mineralization and the accumulation of organic matter creates unsuitable conditions for tree regeneration (Bell 1991, Johnson 1992, Nguyen-Xuan *et al.* 2000, Charron and Greene 2002). Increased depth of humus layers through succession has negative effects on seedling germination and survival (Galipeau *et al.* 1997, Bauhus *et al.* 1998, Cornett *et al.* 1998, Côté *et al.* 2000). Our results suggest a complex successional trend for the thickness of the organic horizons. Organic layers increased in depth at the gap stage. The L-horizon, composed of recently deposited and undecomposed leaf litter, did not change thickness through SDSs. The F-horizon, a prominent feature of northern soils, dominated the organic profiles. The H-horizon became thicker, 5 to 8 cm, and occurred on almost all plots at the gap stage. The biggest increase in thickness was predictably found on moist soils. The progressive accumulation of organic matter underneath old conifer stands has been described as soil degradation (decrease in quality) (Finer *et al.* 1997, Bauhus *et al.* 1998, Côté *et al.* 2000). However, a thicker H-horizon can enrich mineral soils when the uprooting of trees mixes the organic and mineral layers, creating high-quality seedbeds for regeneration (Charron and Greene 2002).

The degree of decomposition and mixing of the humus layer as well as its thickness in a soil profile affect tree regeneration. Mulls provide better seedbeds than moders or mors (Bergeron and Dubuc 1989, Kuusela 1990, Bell 1991). However, the richest humus form, mulls, was infrequent on boreal mixedwood sites and associated only with early SDSs. At these stages, hardwood leaf litter can be quickly transformed into mull humus because of a faster rate of decomposition by soil invertebrates and fungi. More acid conditions along with conifer needle litter under shaded (colder) conditions promotes slower decomposition (Prescott *et al.* 2000), resulting in the prevalence of moders or mors on the majority of sites, especially at the late successional stage.

Table 10. P-values from analysis of variance of organic soil horizons for total depth and depth of L-, F- and H-horizons by stand development stage (D_j) and broad soil group (S_j).

Source	All horizons	L-horizon	F-horizon	H-horizon
D_j	0.03	0.95	0.28	0.04
S_j	0.03	0.94	0.54	0.006
$D \times S_j$	0.50	0.46	0.91	0.21

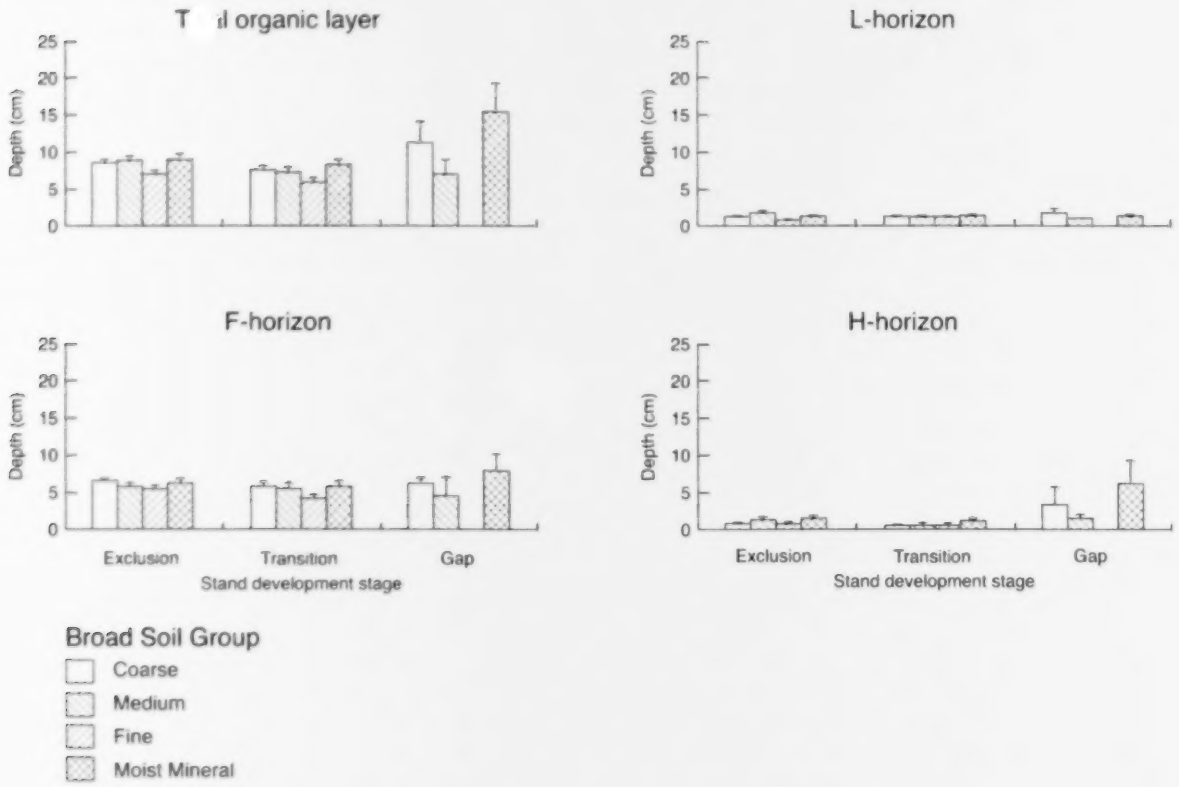

Figure 24. Depth of organic horizons in relation to stand development stage and broad soil group.

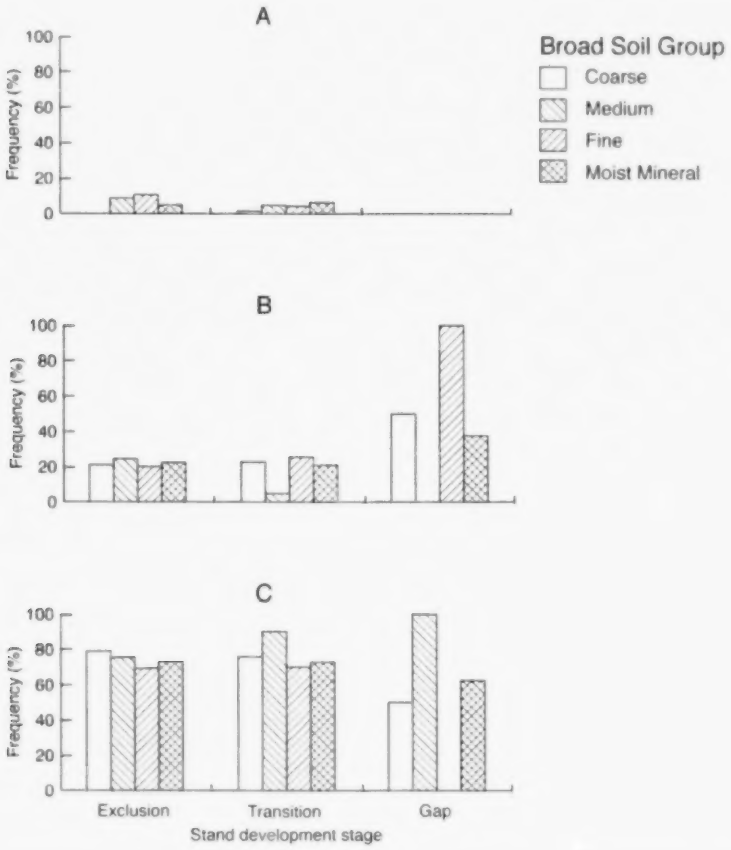

Figure 25. Humus form frequency in relation to stand development stage and broad soil group for: A) mull, B) moder and C) mor.

Snags

Snag (dbh ≥10 cm) density varied significantly with SDS and BSG with the highest densities at the transition stage on medium soils (Table 11 and Figure 26). Small snags (dbh between 10 to 20 cm) accounted for the majority of snags and varied significantly with SDS and BSG and had a similar pattern to the density of all snags. Medium snag (dbh between 20.1 and 30 cm) and large snag (dbh >30 cm) densities did not significantly differ between SDSs or BSGs (Table 11 and Figure 26).

Snag density varied greatly among species (Figure 27). Jack pine and trembling aspen snags were abundant at the exclusion and transition stages and at very low densities at the gap stage. The low snag density of these species could be a factor of size. Large stems are more likely to blow down rather than die while standing, and hence, are lost from the snag class. Both species decreased in density between the exclusion and transition stages for all BSGs. Balsam poplar snag density was low for all SDSs and BSGs. White birch and black spruce snag density did not differ with SDS or BSG. White spruce and balsam fir snag density increased with stand development, and the highest densities for both species were at the gap stage (Table 12). White cedar snags were only found at the gap stage on moist soils. Snags of other species were very rare and were only found in the first two stand development stages (Figure 27).

Table 11. P-values from analysis of variance of snag density (dbh >10 cm) in relation to stand development stage (D_i) and broad soil group (S_j).

Source	All snags	Small snags (dbh 10–20 cm)	Medium snags (dbh 20.1–30 cm)	Large snags (dbh >30 cm)
D_i	<0.001	<0.001	0.37	0.11
S_j	<0.001	<0.001	0.86	0.11
$D \times S_{ij}$	<0.001	<0.001	0.91	0.40

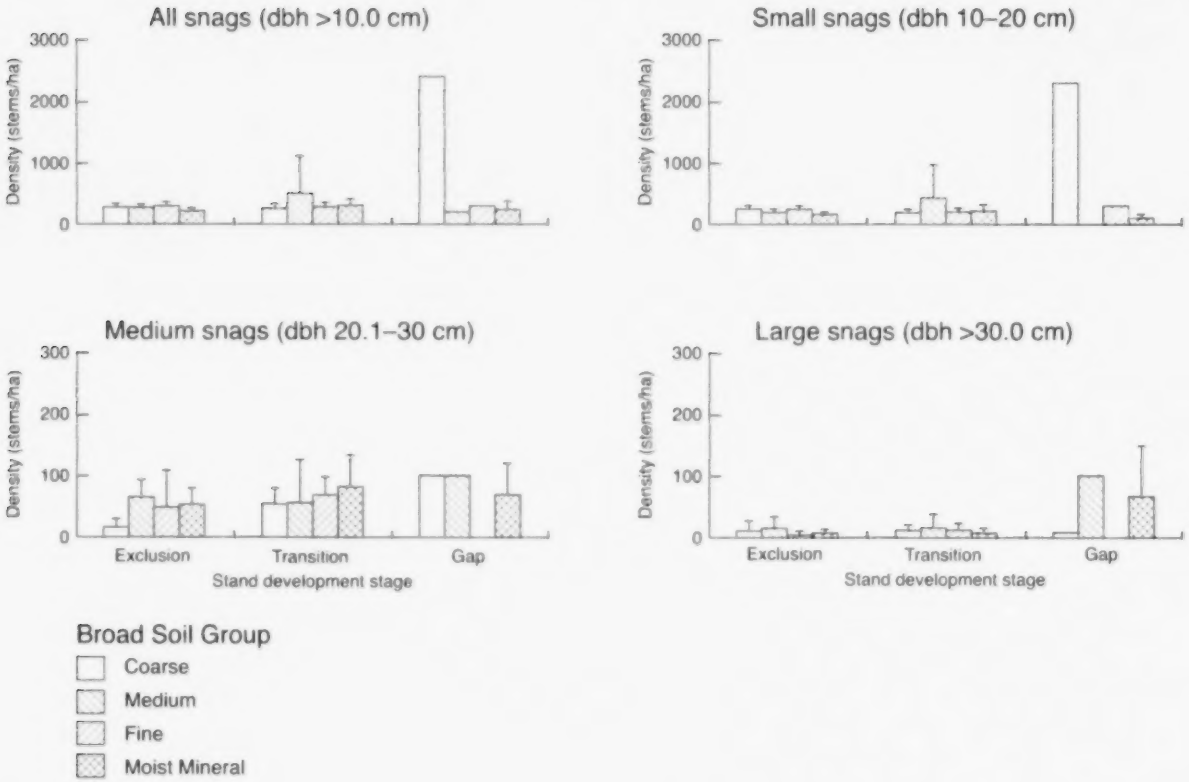

Figure 26. Snag density in relation to stand development stage and broad soil group.

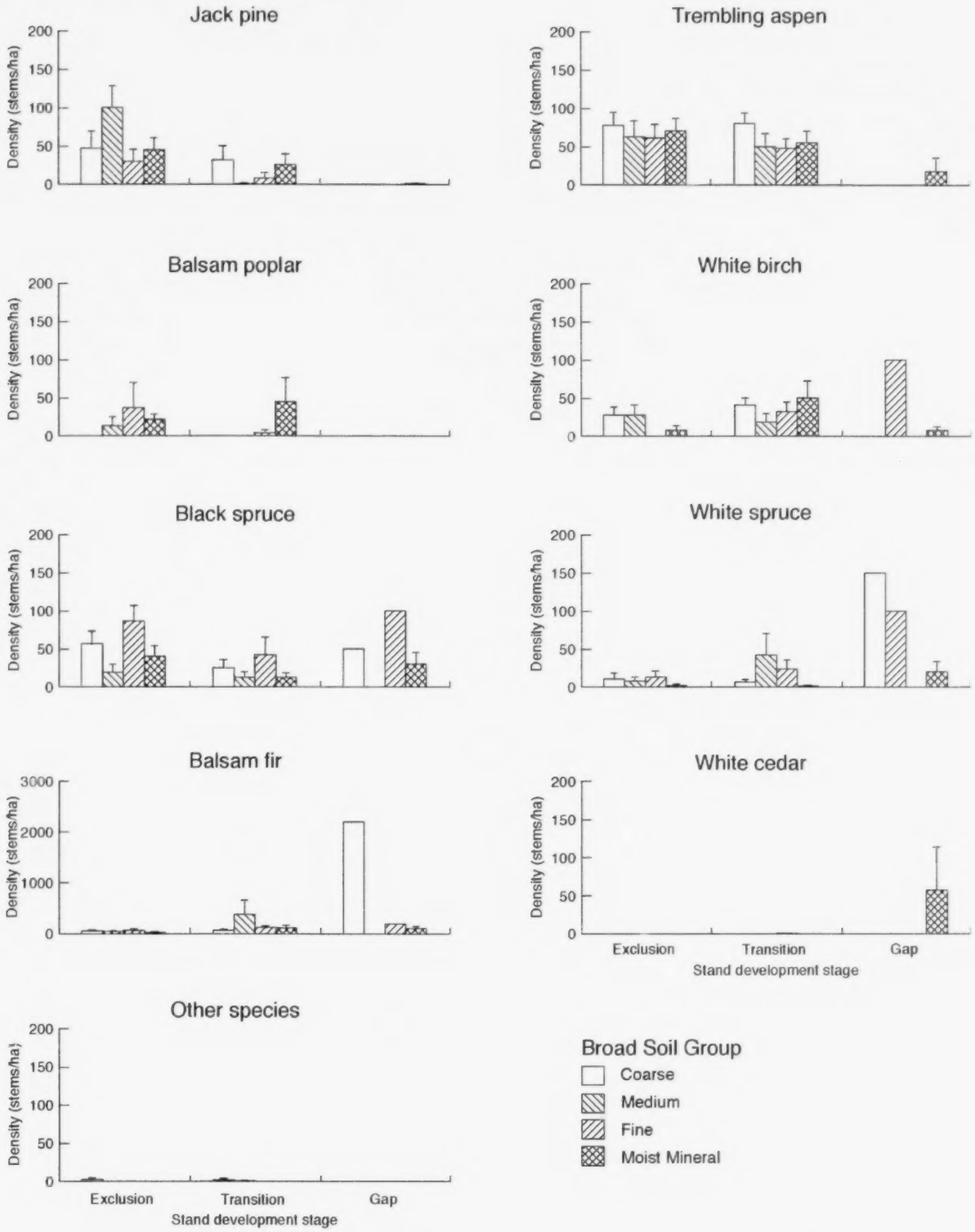

Figure 27. Species-specific total snag density in relation to stand development stage and broad soil group.

Table 12. P-values from analysis of variance of species-specific density of snags in relation to stand development stage (D_i) and broad soil group (S_j).

Source	Jack pine	Trembling aspen	Balsam poplar	White birch	Black spruce	White spruce	Balsam fir	White cedar	Other
All snags									
D_i	0.03	0.32	0.82	0.08	0.10	0.001	<0.001	0.40	0.96
S_j	0.98	0.97	0.87	0.63	0.43	0.001	<0.001	0.01	0.94
$D \times S_{ij}$	0.75	0.99	0.74	0.38	0.98	0.007	<0.001	0.06	1.0
Small snags (dbh 10–20 cm)									
D_i	0.02	0.32	0.58	0.20	0.07	0.16	<0.001	0.55	0.97
S_j	0.97	0.99	0.83	0.93	0.32	0.004	<0.001	0.95	0.95
$D \times S_{ij}$	0.75	0.99	0.96	0.44	0.93	0.007	<0.001	0.66	1.0
Medium snags (dbh 20.1–30 cm)									
D_i	0.76	0.73	0.96	0.21	0.85	<0.001	0.12	0.40	N/A
S_j	0.99	0.99	0.93	0.89	0.46	<0.001	0.50	0.01	N/A
$D \times S_{ij}$	0.98	0.64	0.44	0.99	0.63	<0.001	0.33	0.06	N/A
Large snags (dbh >30 cm)									
D_i	0.79	0.96	0.61	<0.001	0.77	0.26	0.43	0.40	0.77
S_j	0.99	0.78	0.99	<0.001	0.98	0.44	0.20	0.01	0.98
$D \times S_{ij}$	0.83	0.93	0.96	<0.001	0.90	0.51	0.23	0.06	0.90

Species-specific density of small snags had a similar relationship to SDS and BSG as total snag density since small snags accounted for the majority of snags (Figure 28). The only difference was that small white spruce snags were not affected by SDS and no small white cedar snags were found. Medium snags of jack pine, trembling aspen and balsam poplar occurred only at the exclusion and transition stages while white birch, black spruce and balsam fir snags occurred at all three stages (Figure 29). The density of medium white spruce snags increased with stand development and was highest at the gap stage on coarse and moist soils and differed between soil types on the other two stages (Figure 29). Balsam fir snags were present on all SDSs and BSGs, but did not differ among SDSs or BSGs. White cedar snags occurred only at the gap stage on moist soils. Large snag density was low for all species and did not differ among SDSs and BSGs for most species except for white birch and white cedar. White birch

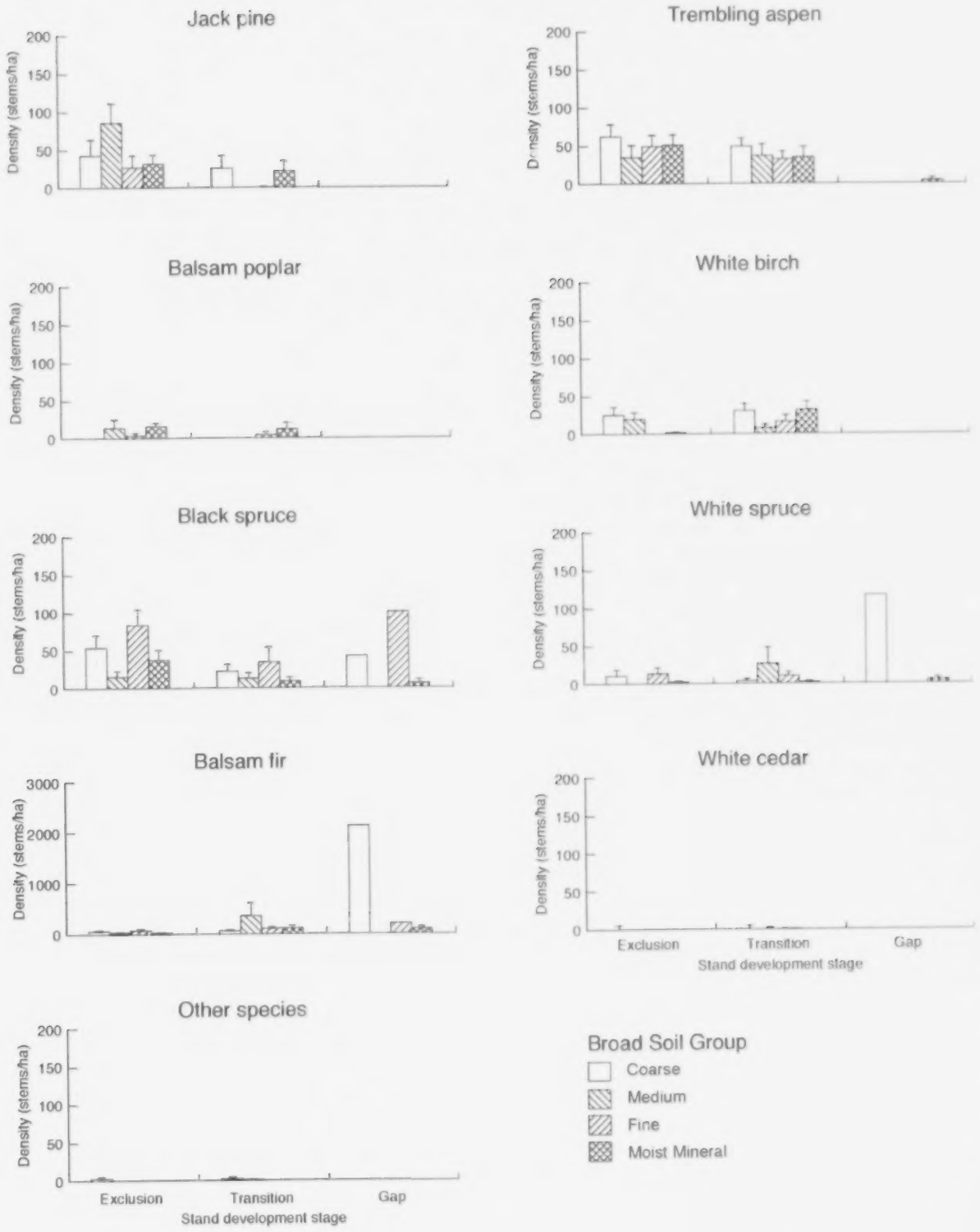

Figure 28. Species-specific small snag (dbh 10–20 cm) density in relation to stand development stage and broad soil group.

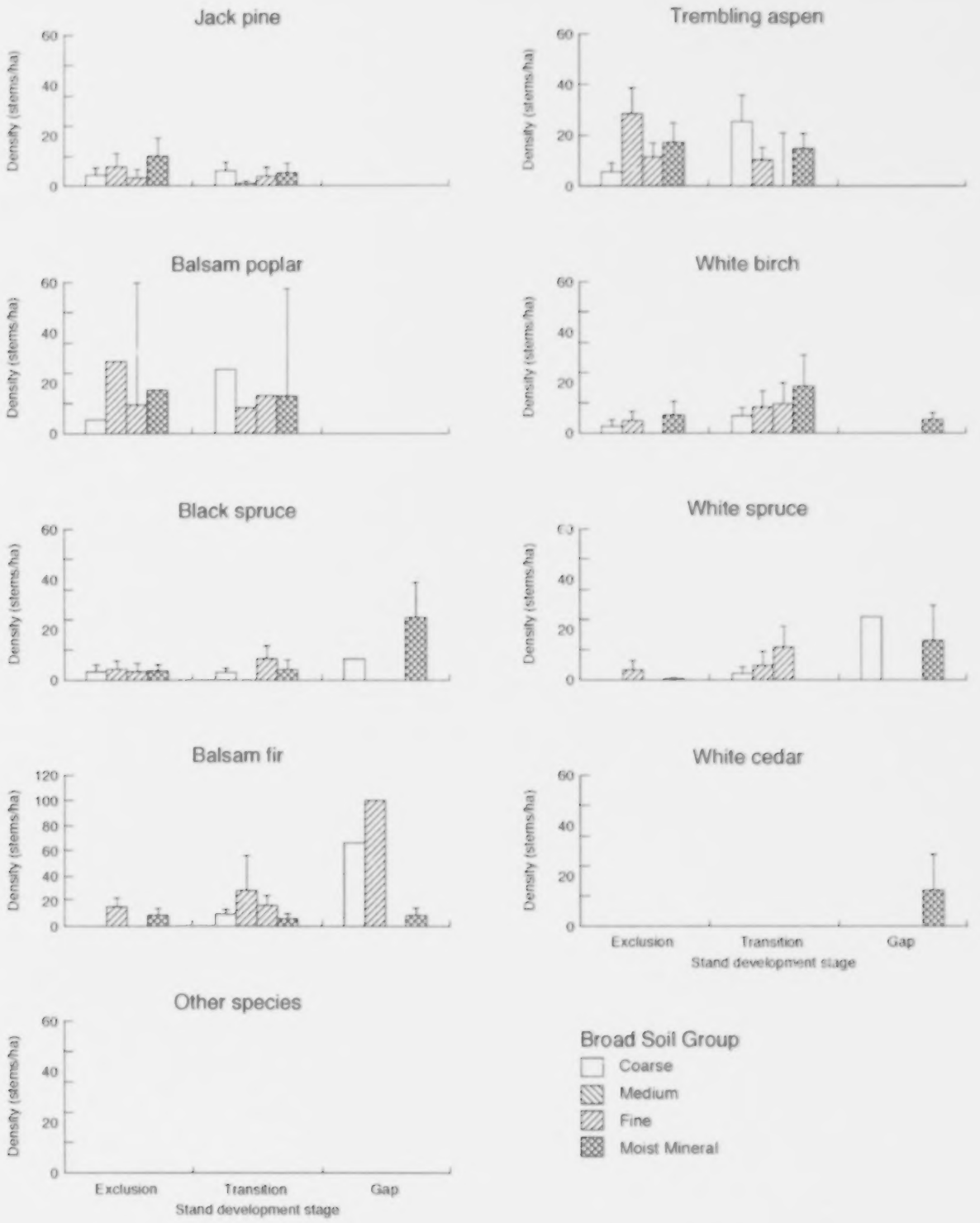

Figure 29. Species-specific medium snag (dbh 20.1–30 cm) density in relation to stand development stage and broad soil group.

large snag density was highest at the gap stage on medium soils. Large white cedar snags occurred only at the gap stage on moist soils (Figure 30).

Snags are the result of mortality through competition, senescence, or non-stand-replacing disturbances. Snags are an important part of forest ecosystem structure and increase the diversity of bird and small mammal communities (Spytz 1993, Schieck *et al.* 1996, Lee *et al.* 1997, Hobson and Schieck 1999, Hely *et al.* 2000). On Ontario's boreal mixedwood sites, snag densities were within the range given for other boreal forests (e.g. Hely *et al.* 2000). On coarse soils, the successional trend of snag density followed the asymmetrical U-shaped pattern that was found with aspen snags in southwestern Quebec (Hely *et al.* 2000). The pattern is characterized by a high density of snags at early successional stages, few snags in the intermediate stages and a high density at the later stages of succession. On medium soils, the pattern of change in density was similar to that on coarse soils but with a much lower magnitude. On fine and moist soils, snag density did not change with SDS. The lack of a consistent trend among BSGs is likely related to the diverse causes of tree mortality and differences in species-specific snag persistence, as snag longevity before falling over can vary with species by decades (Bergeron and Charron 1994).

Individual species varied in contribution to total snag density. Trembling aspen, black spruce and balsam fir snags were the most numerous, corresponding to aspen and black spruce live stem density. At the gap stage, higher snag densities of white birch, black spruce, white spruce and balsam fir than at the other stages possibly indicate that their mortality was a result of senescence rather than competition. The high density of balsam fir snags also reflects the mortality from spruce budworm (*Choristoneura fumiferana* (Clem.)) defoliation in the 1980s. Medium and large snags were sporadic in boreal mixedwoods, but were present on all SDSs and BSGs.

Conclusions

The successional shift in species composition among stem exclusion, canopy transition and gap dynamics stages was evident in Ontario's boreal mixedwoods. Stand basal area increased from exclusion to transition to gap dynamics stage and it was higher on medium and fine soils than on coarse and moist mineral soils. Stand density decreased from stem exclusion to transition to gap dynamics stage on coarse, medium and moist mineral soils. The most frequently occurring saplings and seedlings were balsam fir and black spruce, followed by white spruce and white birch. White cedar saplings and seedlings were frequent only at the gap dynamics stage while trembling aspen and balsam poplar saplings were frequent at the stem exclusion and transition stages.

Shrubs and non-woody vegetation occurred frequently on all sites and at all stand development stages. Shrub cover was significantly higher at the gap dynamics stage than the exclusion and transition stages. Herbs and mosses were the most abundant non-woody vegetation. Mean depth of the surface organic layer varied from 7 to 15 cm. The humus layer was thickest at the gap dynamics stage. Mor was the most frequent humus form, followed by moder while mull was infrequent. Snag density varied greatly between stand development stages and broad soil groups and the majority were small snags (dbh between 10 to 20 cm). Snags of early-successional jack pine, trembling aspen and balsam poplar occurred mostly at the exclusion and transition stages, mid-successional white birch and black spruce occurred at all stages and late-successional white spruce, balsam fir and white cedar were most frequent at the gap dynamics stage.

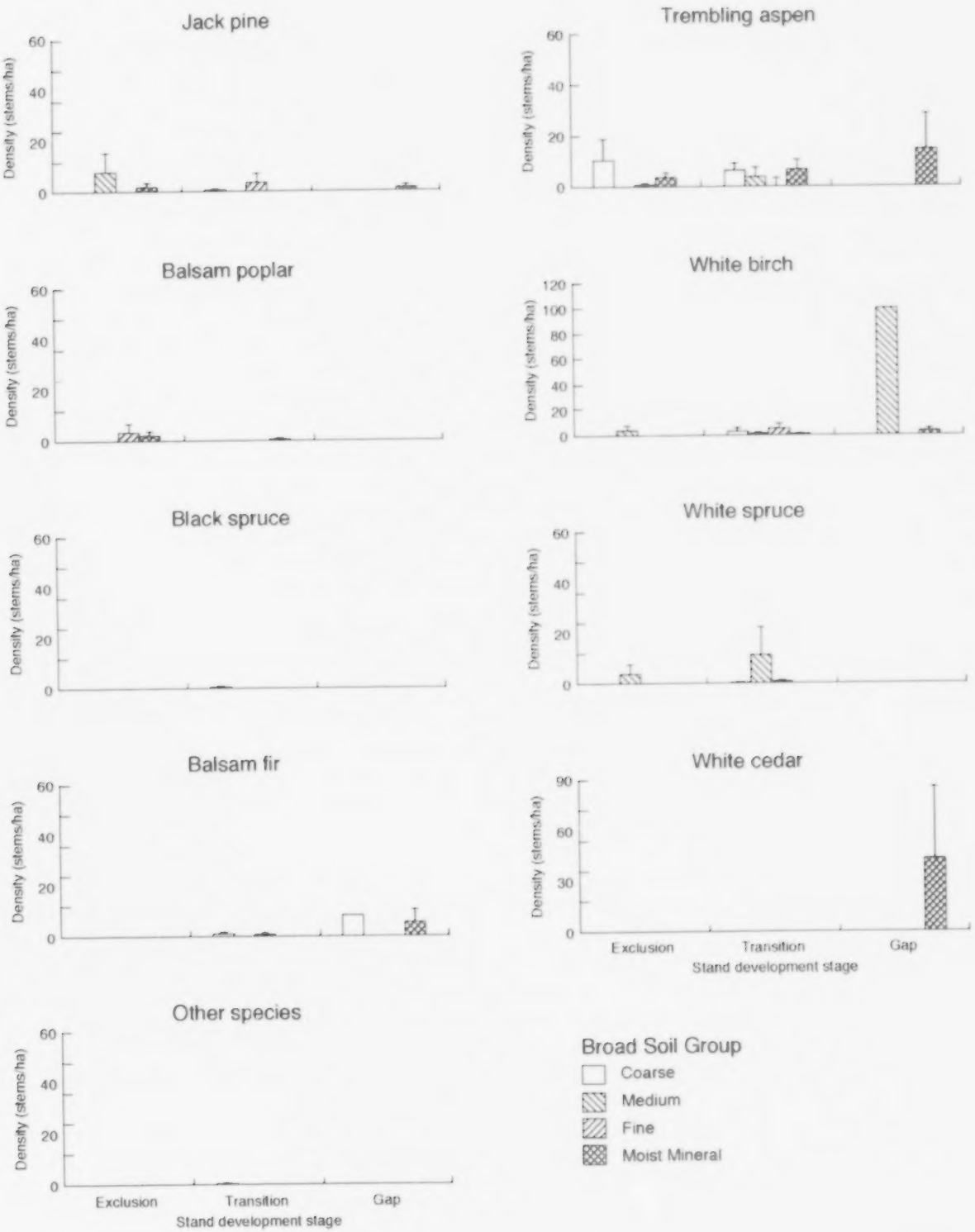

Figure 30. Species-specific large snag (dbh >30 cm) density in relation to stand development stage and broad soil group.

The historical databases allowed us to undertake this study. However, limitations associated with those historical databases inevitably affected the scope and types of questions that we could address in this report. To further improve our understanding of Ontario's boreal mixedwoods, future efforts need to be undertaken through various provincial initiatives to:

- Collect data to improve our understanding of stand initiation and gap dynamics stages.
- Implement a standard for data collection to ensure that future efforts can be used beyond individual projects.
- Strategically collect data recognizing that climate and initial compositional types may significantly affect stand dynamics.

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APPENDICES

Appendix 1. Sample sizes for all stand attributes

Table A1. Number of plots for stand age.

	Stand development stage			
Broad soil group	**Exclusion**	**Transition**	**Gap**	**Total**
Coarse	186	115	8	309
Medium	146	88	1	235
Fine	92	55	1	148
Moist	222	89	16	327
Total	646	347	26	1019

Table A2. Number of plots for stand basal area, composition and stand density.

	Stand development stage			
Broad soil group	**Exclusion**	**Transition**	**Gap**	**Total**
Coarse	186	118	8	312
Medium	148	90	2	240
Fine	93	57	1	151
Moist	224	89	17	330
Total	651	354	28	1033

Table A3. Number of plots for sapling frequency.

	Stand development stage			
Broad soil group	**Exclusion**	**Transition**	**Gap**	**Total**
Coarse	149	96	3	248
Medium	95	32	2	129
Fine	89	56	1	146
Moist	148	59	17	224
Total	481	243	23	747

Table A4. Number of plots for sapling density.

	Stand development stage			
Broad soil group	**Exclusion**	**Transition**	**Gap**	**Total**
Coarse	31	50	1	82
Medium	54	17	0	71
Fine	9	18	0	27
Moist	63	27	13	103
Total	157	112	14	283

Table A5. Number of plots for seedling frequency and density.

	Stand development stage			
Broad soil group	**Exclusion**	**Transition**	**Gap**	**Total**
Coarse	6	25	1	32
Medium	7	6	0	13
Fine	2	9	0	11
Moist	14	14	4	32
Total	29	54	5	88

Table A6. Number of plots for shrub frequency and cover (not stratified by size classes).

	Stand development stage			
Broad soil group	**Exclusion**	**Transition**	**Gap**	**Total**
Coarse	127	74	3	204
Medium	51	22	2	75
Fine	86	48	1	135
Moist	102	46	8	156
Total	366	190	14	570

Table A7. Number of plots for non-woody vegetation frequency and cover (not stratified by size classes).

	Stand development stage			
Broad soil group	**Exclusion**	**Transition**	**Gap**	**Total**
Coarse	81	58	2	141
Medium	26	17	0	43
Fine	40	23	0	63
Moist	43	26	4	73
Total	190	124	6	320

Table A8. Number of plots for non-woody vegetation frequency and cover.

	Stand development stage			
Broad soil group	**Exclusion**	**Transition**	**Gap**	**Total**
Coarse	126	65	3	194
Medium	51	20	2	73
Fine	86	47	1	134
Moist	102	44	7	153
Total	365	176	13	554

Table A9. Number of plots for species-specific shrub frequency and cover.

	Stand development stage			
Broad soil group	**Exclusion**	**Transition**	**Gap**	**Total**
Coarse	127	72	3	202
Medium	51	21	2	74
Fine	86	48	1	135
Moist	102	46	8	156
Total	366	187	14	567

Table A10. Number of plots for species-specific non-woody plant frequency and cover.

	Stand development stage			
Broad soil group	**Exclusion**	**Transition**	**Gap**	**Total**
Coarse	121	47	2	170
Medium	44	15	2	61
Fine	84	38	1	123
Moist	87	32	4	123
Total	336	132	9	477

Table A11. Number of plots for depth of organic layers.

	Stand development stage			
Broad soil group	**Exclusion**	**Transition**	**Gap**	**Total**
Coarse	115	71	3	189
Medium	46	20	2	68
Fine	56	34	0	90
Moist	75	36	6	117
Total	292	161	11	464

Table A12. Number of plots for humus form frequency.

	Stand development stage			
Broad soil group	**Exclusion**	**Transition**	**Gap**	**Total**
Coarse	124	75	2	201
Medium	41	21	1	63
Fine	85	47	1	133
Moist	103	48	8	159
Total	353	191	12	556

Table A13. Number of plots for total and species-specific snag density.

	Stand development stage			
Broad soil group	**Exclusion**	**Transition**	**Gap**	**Total**
Coarse	38	39	1	78
Medium	26	9	1	36
Fine	30	26	1	57
Moist	57	25	7	89
Total	151	99	10	260

Appendix 2. Results of K-means cluster analysis on classification of canopy and sub-canopy trees using G&Y plots

Crown class provides an integral estimate of vertical stratification of a stand using direct observations of each tree. This information was available from permanent G&Y sample plots and the latest American Can measurements. We used these plots to test how well K-means cluster analysis classified canopy and sub-canopy trees for each stand based on dbh (Table A14).

Table A14. Percentage of correctly classified crown classes from dbh using K-means cluster analysis for selected G&Y plots.

	% of correctly classified	
Plot	**Canopy**	**Sub-canopy**
BP9306	98.3	84.2
BP9310	57.9	91. 7
BP9317	86.4	94.6
BP9319	100	93.2
BP9323	90	82.5
BP9325	79.9	85.5
BP9331	51.3	92.4
BP9340	55.3	96.9
BP9402	75.1	90.6
CHA9501	88.5	87. 9
CHA9503	75.7	95.7
CHA9504	100	83.0
CHA9512	61.2	88.8
CHA9515	71.3	96.2
CHA9516	30.4	100
CHA9519	100	88.3
CHA9520	53.8	100
CHA9522	96.4	89.8
CHA9526	98.5	91.1
CHA9527	72.1	97.1
Average	77.1	91.5